

Brachiopod assemblages in the Devonian Kowala Formation of the Holy Cross Mountains

GRZEGORZ RACKI



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Brachiopod faunas from the Devonian stromatoporoid-coral series (Kowala Formation) of the southern Holy Cross Mts comprise at least 60 species, atrypids and ambocoeliid spiriferids being the most common. Largely monospecific bottom-level pioneer assemblages colonized intershoal and open shelf environments of the Late Givetian Sitkówka bank complex to the Frasnian Dyminy reef complex, and some lagoonal habitats of the older Givetian *Stringocephalus* bank. The associations dwelling organic buildups were more diverse and specialized. Faunal dynamics of the brachiopods were controlled primarily by eustatic cycles and the evolution of the carbonate shelf. Generally this was a four-step succession from the stringocephalid to the ambocoeliid, atrypid (or cyrtospiriferid), and rhynchonellid faunas. Twenty two species are reviewed, *Praewaagenoconcha(?) sobolevi* sp. n., *Desquamatia globosa aequiconvexa* subsp. n., and *D. g. sitkowkensis* ssp. n. are proposed. Two poorly-known species of Gürich (1896), *Tenticospirifer lagoviensis* and *Ilmenia(?) elattor*, are redescribed.



Key words: brachiopods, taxonomy, paleoecology, Devonian, Poland.

Grzegorz Racki, Katedra Paleontologii i Stratygrafii, Uniwersytet Śląski, ul. Będzińska 60, 41-200 Sosnowiec, Poland.

Introduction

Brachiopod-dominated faunas within the stromatoporoid-coral series (Kowala Formation; see Racki 1993) in the Devonian Kowala Formation of the Holy Cross Mountains are still poorly known. Despite the long history of studies, the brachiopods have been studied only in few localities (Biernat 1969, 1971; Baliński 1973; Racki & Baliński 1981; Racki 1985; Godefroid & Racki 1990).

The present paper is a modified version of my doctoral thesis (Racki 1982) and presents a summary of the present knowledge on this fossil group with special emphasis on ecologic and stratigraphic aspects.

The materials are stored at the Department of Earth Sciences of the Silesian University in Sosnowiec (Catalogue Numbers GIUS-4).

Localities and material

The oldest Givetian brachiopods were derived from widely separated sites such as Sowie Górki (sets A-B; see the locality register in Racki 1993) and Ołowianka (set A), Czarnów (set A; Filonowicz 1967), Laskowa (set A₁; Racki *et al.* 1985) and Jurkowiec-Budy (Baliński 1973), as well as from Dzięwki near Siewierz (Baliński 1971). All the localities represent the *Stringocephalus* Beds, and their Silesian equivalent the Dzięwki Limestone. The upper part of this bank-type deposits, and the overlying open-shelf Jaźwica Member has appeared the most fossiliferous, especially in the sections of Jaźwica-Góra Łgawa, Góra Zamkowa, Bilcza hills, Stokówka, Pośłowice and Marzysz. Two localities in the eastern part of the region (Łagów, Wojnowice-Podgórze) yield possibly coeval late Givetian assemblages.

The Givetian to Frasnian passage beds, developed in intershoal (Chęciny Beds) and various biostromal (lower Sitkówka Beds) facies, were extensively sampled in several outcrops, mainly in environs of Chęciny (e.g. Góra Zamkowa, Zegzelogóra), and Sitkówka (Pośłowice, set C; Sitkówka-Kostrzewa). The Early Frasnian is represented in the upper Sitkówka Beds and Kadzielnia Member, and prolific sites comprise Kowala, Jaźwica (sets H-J) and Miedzianka (e.g. Sowie Górki, set F).

The Middle Frasnian onlap (*Phlogoiderhynchus* Marly Level) is the upper limit of the sequence covered by this study. Only some sparse associations from amphiporid sequences (e.g. Jaworznia) of the Frasnian, of not precisely determined age, are included.

The brachiopod collection examined comprises above 3000 differently preserved specimens gathered from varied, but predominantly compact, limestone lithologies. Some specimens were recovered by washing of weathered rock (Jurkowiec-Budy; Jaźwica, set H; Jaworznia) and chemical processing of silicified remains (Sitkówka-Kostrzewa, Siewierz). Abundant and well preserved material has been obtained from marly partings and interbeds from the Jaźwica Member. Minute phosphatic shells of the lingulids have been found in some acid-resistant residues; frequent and well preserved remains are limited in occurrence to the Jaźwica Member (Pośłowice, Trzemoszna), and in first order to the *Phlogoiderhynchus* Level (Kowala, Jaźwica).

Taxonomical review of faunas

Only the species that are quite numerously represented in the series under study are here presented. Sparingly occurring taxa, contributing less than

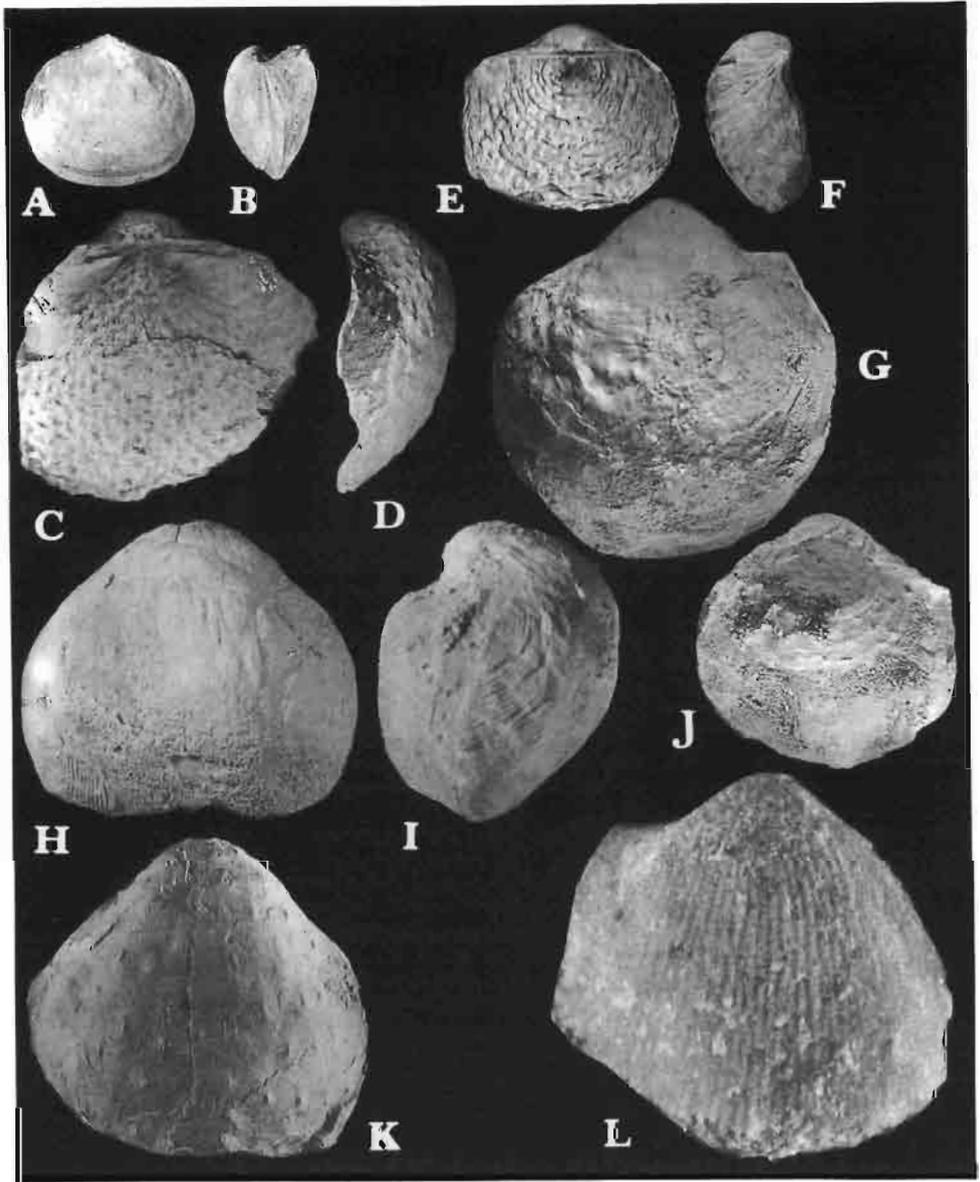


Fig. 1. A-B. *Schizophoria* sp. B, ventral and lateral views, GIUS 4-251/S-1; Frasnian upper Sitkówka Beds, Jaźwica (set H). C-F. *Praewaagenoconcha*(?) *sobolevi* sp.n., dorsal and lateral views, GIUS 4-217/P-2 (C-D), GIUS 4-215/P-1 (E-F); Givetian Jaźwica Mbr., Posłowice (set B; C-D), Marzysz (E-F). G, J-K. *Productella* cf. *subaculeata* (Murchison 1840), ventral and dorsal views, GIUS 4-245/P-1, 2; Frasnian Chęciny Beds, Góra Zamkowa (easternmost outcrop; set I). H-I. *Schizophoria* aff. *mcfarlanei* (Meek 1868), ventral and lateral views, GIUS 4-219/S-1; Givetian lower Sitkówka Beds, Trzemoszna. L. *Rhyssochonetes* cf. *meneri* (Lyashenko 1959), ventral view, GIUS 4-230/O-1; Givetian Chęciny Beds, Zegzelogóra. All $\times 2$ except for L that is $\times 5$.

one per cent to the total collection, are mostly illustrated only (Figs 1-26), and the full list is presented in Fig. 33; this concerns also the species that have already been elaborated (Biernat 1969, 1971; Baliński 1973; Racki & Baliński 1981; Racki 1985).

Schizophoria sp.— Orthids are represented only by species of *Schizophoria*. Large, up to 40 mm width, transversely-outlined and strongly dorsibiconvex variety, designated as *S. sp. A*, is known from the Jaźwica Member (Pośłowice) and overlying coral strata (Trzemoszna; ?also Jaźwica, set C). A small, subequally biconvex form (*S. sp. B*; Fig. 1A-B) with at the best weak sulcus in the dorsal valve occurs solely in the Frasnian units studied (Jaźwica, set H; Kadzielnia, set A; ?also Jaworznia).

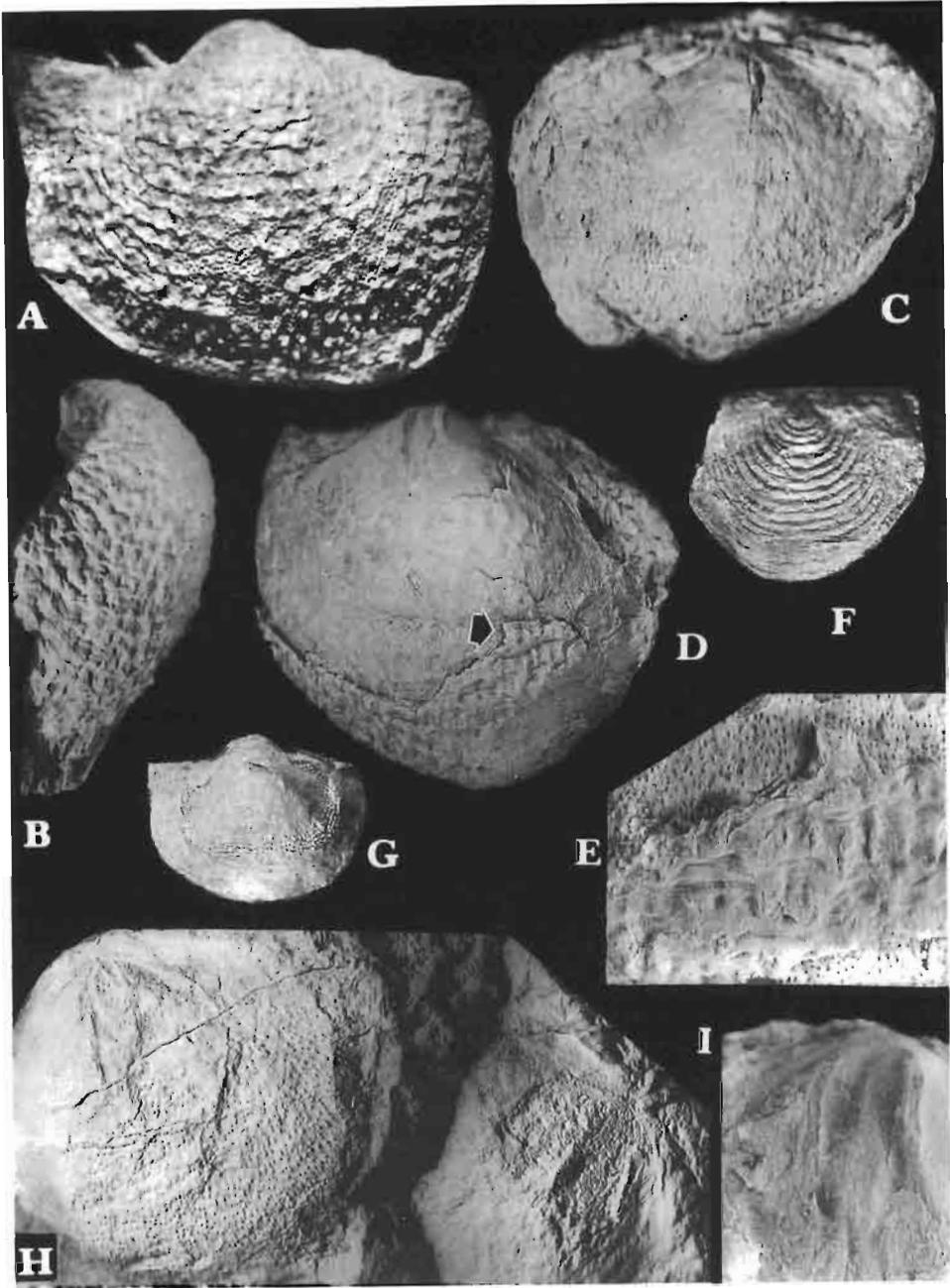
The most characteristic schizophoriids include gypidulid-like specimens from Trzemoszna (Fig. 1H-I) determined as *S. aff. mcfarlanei* (Meek 1868) (see Warren & Stelck 1956; Johnson 1974). The Holy Cross Mountains specimens differ from the North American species in smaller size (at comparable ontogenic stages), are wider, and show shallower sulcus.

Productella cf. subaculeata (Murchison 1840) (Fig. 1G, J-K).— Two damaged shells, 10 ventral and 3 dorsal valves, mostly embedded in the rock, have been found in the Chęciny Beds (Góra Zamkowa, set I; ?also Zegzelogóra, Sosnowka, set C, Góra Zamkowa, set A). The taxonomic assignment is equivocal because of the scarcity of material, even if the Frasnian specimens from Chęciny are difficult to separate from this widespread species. In the shell shape and spine arrangement they are close to the morphotype 2a recognized in the type locality (the Frasnian of Ferques, N-France) by Brousmiche (1973), but reach an adult size twice as large as the neotype. In this respect the shells resemble rather some Late Devonian populations of the species (Nalivkin 1930, 1947), and *P. 'dutertrei'* Rigaux 1909 from the Frasnian of Ferques (Brousmiche 1973).

Praewaagenoconcha(?) sobolevi sp. n. (Figs 1C-F, 2A-D, E, H-I).— For description see p. 320. The species occurs in the Late Givetian Jaźwica Member at Pośłowice, Marzysz, and maybe also Stokówka. A close form occurs in the Middle Givetian Laskowa Góra Beds at the type section (Racki *et al.* 1985).

Devonoproductus sericeus (von Buch 1837) (Figs 2F-G, 3L-N, S).— The material of one incomplete shell, 8 ventral and 6 brachial valves, embedded in rock and mostly exfoliated, and 15 shell fragments, is regarded as conspecific with the Frasnian Russian specimens (Nalivkin 1947, 1951; Lyashenko 1959) of *D. sericeus*. The Polish form differs only in more sparsely distributed spines on the pedicle valve and slightly longer hingeline. Some specimens with pronounced rows of spines (Fig. 3M) are closer to the Sudetian representatives of the species (Dames 1868). Other morphotypes in the collection have a rather continuous, delicate striation of the pedicle valve (Fig. 3N) being transitional to *D. gracilis* Lyashenko

Fig. 2. □A-D, E, H-I. *Praewaagenoconcha(?) sobolevi* n.sp., holotype GIUS 4-217/P-1 (L=21.5 mm, W=25.1 mm, T=8.5 mm) in ventral and lateral views (A-B); interior of dorsal valves (C,



H). large shell in ventral view (D) and details of its sculpture (E) and muscle field (I), GIUS 4-217/P-3 (C), P-4 (D-E, I), P-6a, b (H); Jażwica Mbr., Givetian, Posłowice (set B). □F-G, *Devonoproductus sericeus* (von Buch 1837), ventral and dorsal views of exfoliated shells, GIUS 4-244/O-1, 2; Frasnian Chęciny Beds, Góra Zamkowa (set I). All $\times 2$ except for E and I that are $\times 5$.

1973 from the Early Frasnian of Russia; however, the shells of both species are essentially unknown internally.

The species occurs in the Late Givetian to earliest Frasnian Chęciny Beds (Zegzelogóra; Góra Zamkowa, set I) and is reported from the Sudetes and the Eifel (undetermined Frasnian), East European Platform, Urals and Kazakhstan (Frasnian, mostly the early half; Lyashenko 1959, 1973).

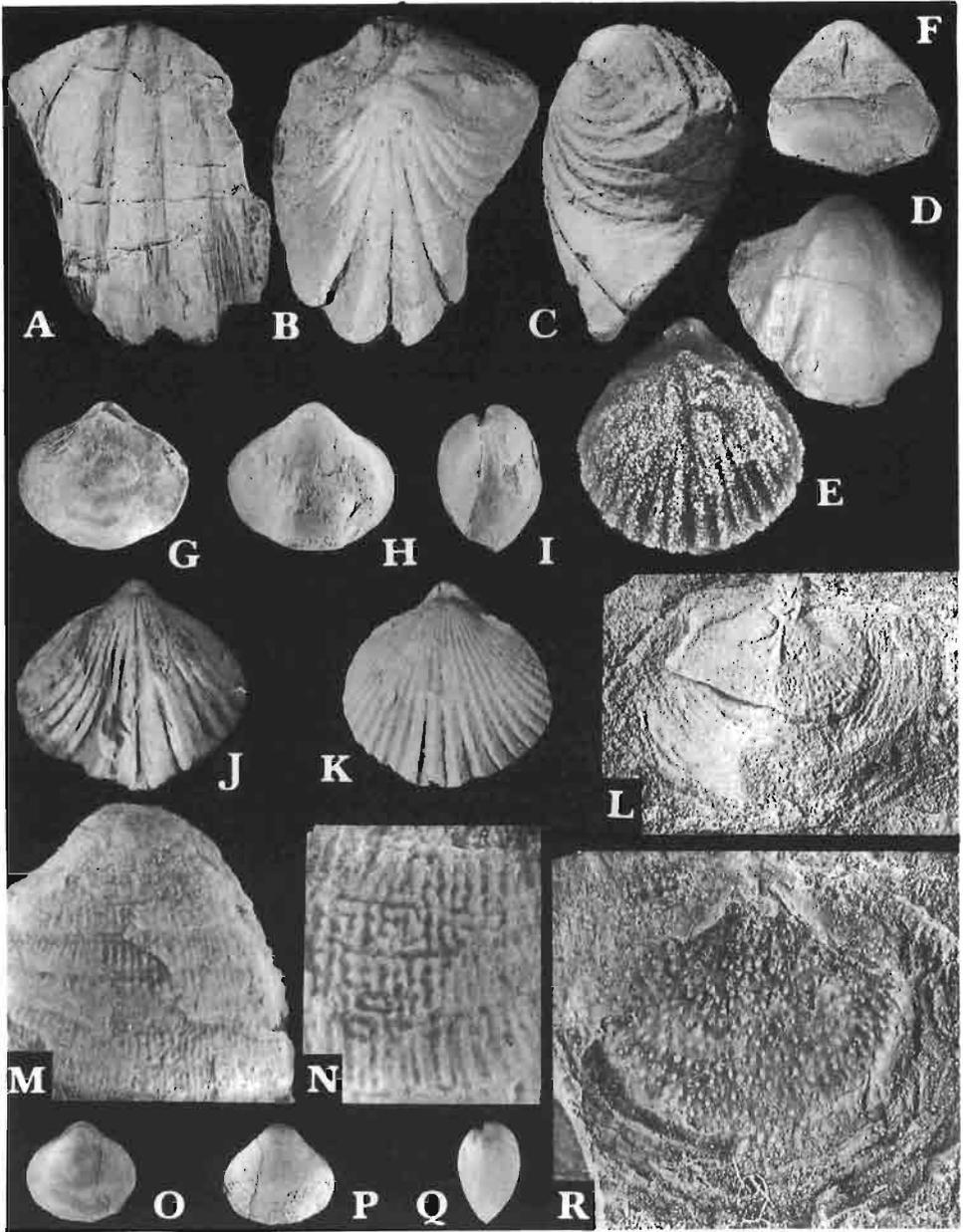
***Metabolipa* sp. ex gr. *M. rectangularis* (Torley 1934)** (Figs 3D, F-I, O-R, 4A).— The collection from the Givetian (?upper *Stringocephalus* Beds) of Wojnowice-Podgórze near Iwaniska includes 7 shells (mostly juveniles), 5 pedicle and 6 brachial valves, above 30 fragments. A few larger-sized shells in the collection, reaching up to 15 mm in length, point to a wide variability in the shell outline and number of costae. Internally, the specimens correspond to *Metabolipa* and might belong to the species group of *M. rectangularis* sensu Jux (1969). Diminutive size combined with a poorly developed sulcus, fold, and costae all suggest a juvenile ontogenetic stage of the examined forms.

The gypidulids from the eastern Holy Cross Mountains have been earlier attributed (Samsonowicz 1917; Ozonkowa 1961) to *Gypidula acutelobata* (Sandberger 1856).

Small-sized gypidulids have been noted only from Kuby-Młyny in the western part of the region as *Gypidula parva* Biernat 1966 by Filonowicz (1973). *M. rectangularis* is known in the Rhenish Slate Mountains from the Givetian and Frasnian (mostly 'Untere Plattenkalk' and 'Massenkalk'; Jux 1969). Specimens from the Frasnian Kadzielnia Limestone, assigned to this species by Biernat (1971), belong probably (Godefroid & Racki 1990) to *M. greindli* (Maillieux 1909).

***Ripidiorhynchus* aff. *pskovensis* (Nalivkin 1940)** (Figs 3A-C, E, J-K, 4).— Six complete, and 12 damaged and/or deformed shells, and 5 fragmentary valves exhibit a distinctive variation in the shell outline and costal formula, and especially in the shell biconvexity. The last character argues for marked differentiation of growth rate within populations as discussed by Torley (1934). Sobolev (1909) assigned two differently inflated specimens from Góra Zamkowa to separate species *Rhynchonella letiensis* Gosselet 1887 (actually restricted to the Famennian and later placed in the genus *Centrorhynchus*) and *R. aff. ferquensis* Gosselet 1887. The latter Frasnian species from Boulonnais, France, probably widespread at least in Europe (Brice 1982) has significantly diminutive (length up to 11.5 mm), and rather transversely elongated and flattened shells, and shows deeper umbonal cavities (Brice & Meats 1971). Therefore, similarly-sized *R. pskovensis* from the earliest Frasnian (Sargaievo horizon) of the Russian Main Devonian Field seems to be more allied to the Holy Cross Mountains species; most of the specimens examined resemble the one figured by

Fig. 3. □A-C, E, J-K. *Ripidiorhynchus* aff. *pskovensis* (Nalivkin 1941), strongly inflated shell in anterior, posterior and lateral views (A-C), juvenile specimen in ventral view (E), and dorsal view of flattened shells (J-K), GIUS 4-216/R-1(A-C), R-12 (E), R-3 (K), GIUS 4-213/R-1 (J);



Givetian Jaźwica Mbr., Góra Zamkowa (set A₂: A-C. E. K); Stokówka (set B: J); × 2 except for E that is × 5. □D, F-I, O-Q. *Metabolipa* ex gr. *rectangularis* (Torley 1934), ventral valves in external and internal views (D, F), and small shells in dorsal, ventral and lateral views (G-I, O-Q), GIUS 4-178/16 (D), 13 (F), 1 (G-I), 2 (O-Q); Givetian ?*Stringocephalus* Beds, Wojnowice-Pogórze: × 2. □L-N, R. *Devonoproductus sericeus* (von Buch 1837), dorsal interiors (L, R), damaged shell in ventral view (M: N – details of ornamentation), GIUS 4-230/O-6 (L), GIUS 4-244/O-3 (M-N), O-4 (R); Givetian (M) and Frasnian (N) Chęciny Beds, Zegzelogóra (set ?B: L) and Góra Zamkowa (middle outcrop, set I: M-N, R); × 5 (L-M, R) and × 10 (N).

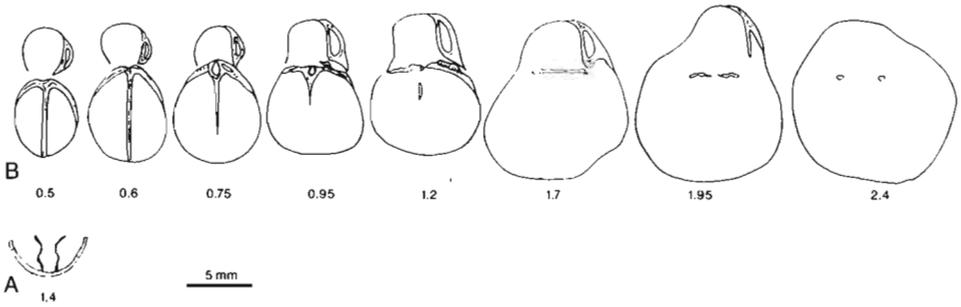


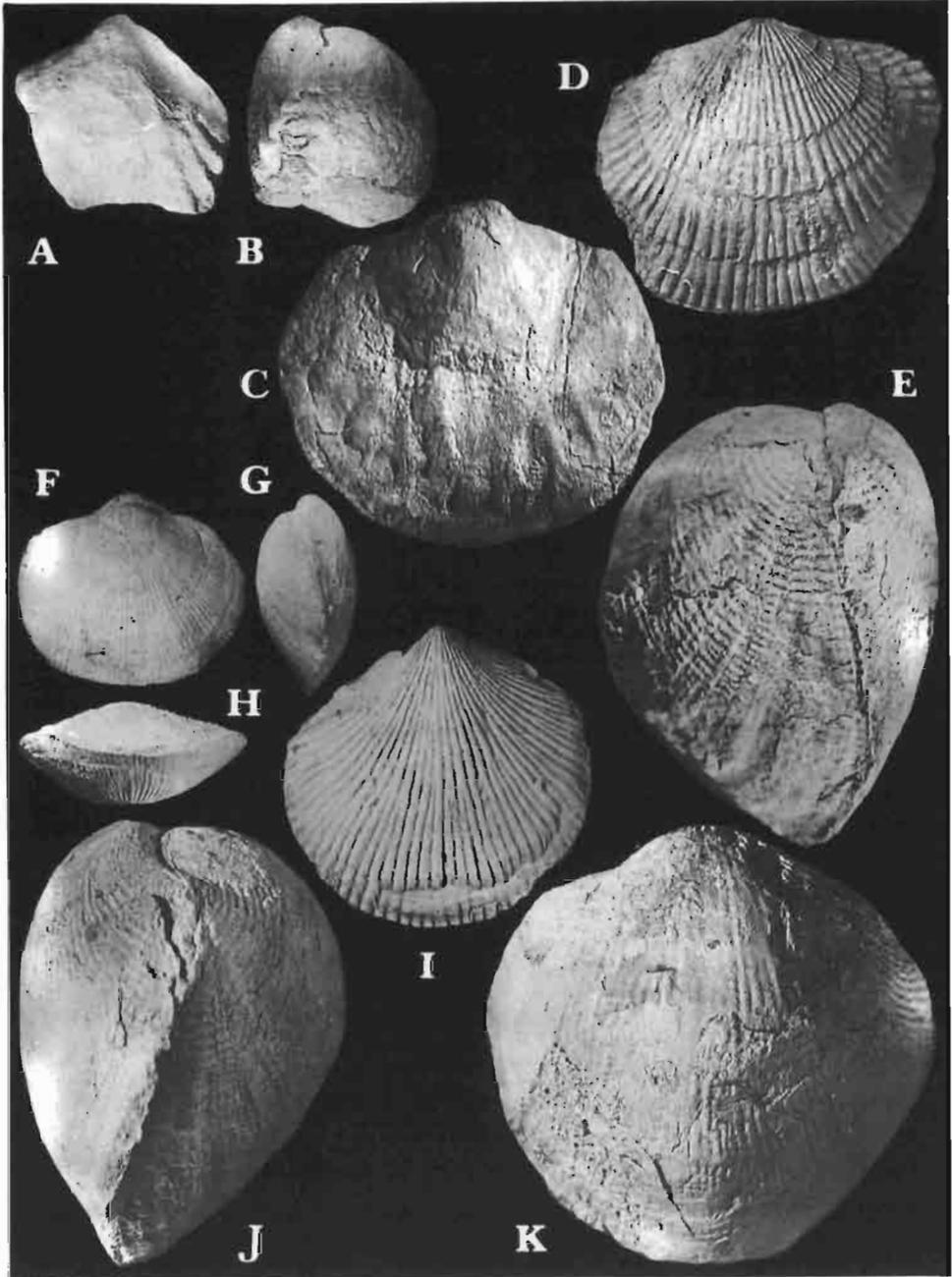
Fig. 4. Serial sections of *Metabolipa* ex gr. *rectangularis* (dorsal valve, GIUS 4-178/16; Givetian ?*Stringocephalus* Beds, Wojnowice-Podgórze; A) and *Ripidiorhynchus* aff. *pskovensis* (GIUS 4-216/R-10; Givetian Jaźwica Mbr., Góra Zamkowa, set A₂).

Nalivkin (1940: Pl. 3: 4). Nevertheless, the Russian species displays a few parietal costae (2-3; at most 1 in the Chęciny form) and a tendency to develop a flat to gently concave pedicle valve. Its interior remains unknown. Possibly, the rhynchonellid studied may represent a new species being the oldest, viz. Givetian representative of this genus (Sartenaer 1985).

The species is found in the Late Givetian Jaźwica Member at Góra Zamkowa and Stokówka.

***Desquamatia globosa* (Gürich 1896).**— As already pointed out by Racki (1985) there is a serious ecologic bias in the taxonomy of the whole subfamily Variatrypinae. Biometrics show great variability (Coleman 1951; Copper 1966b; Frost & Langenheim 1966; Jones 1974; Grey 1978) and in the studied strata different 'subgeneric' forms of *Desquamatia* reveal very distinct facies control (ecodemy of Copper 1966b; Copper & Racheboeuf 1967a: pp. 64-66). They are interpreted here as local populations only within particular, widespread and highly adaptable species. Already Copper (1966b: p. 39) claimed that 'these ecologically restricted genera (...) may indeed also be a form of ecophenotype in atrypid taxonomy, i.e. a recurring type of external morphology, dissociated from the major phylogenetic trends, which disappears and reappears with changing environments' (see also comments on 'brachiopod niches' by Wallace 1978 and McGhee 1981). For discussion of the species and revised diagnosis see p. 322. The most common subspecies is *Desquamatia globosa globosa* (Gürich 1896) (Figs 5C,E, J-K, 6-7) which occurs in the Late Givetian to earliest Frasnian strata (Chęciny Beds, ?Sitkówka Beds) at Góra Zamkowa (sets ?B, E-F and J), Sosnowka, Zegzelogóra, Sitkówka-Kostrzewa (set B₁), and possibly also Jaźwica (sets D, H). *Desquamatia globosa aequiconvexa* subsp. n. (Figs 6-7, 8A-F; for description see p. 323) is limited in distribution to the latest Givetian Chęciny Beds (Atrypid-Crinoid Level) and only

Fig. 5. □A-B. *Parapugnax*(?) sp., incomplete shell in ventral and lateral views, GIUS 4-216/O-1; Givetian Jaźwica Mbr., Góra Zamkowa (set A₂). □C, E, J-K. *Desquamatia globosa globosa* (Gürich 1896), internal cast in ventral view (C), large shells in dorsal and lateral views, GIUS



4-230/D-10 (C), D-1 (E), GIUS 4-237/D-1 (J-K): Givetian Chęciny Beds, Zegzelogóra (set B; C, E), Sitkówka (set B₁, bed B-1; J-K). □D. *Desquamatia* cf. *magna* (Grabau 1931), dorsal view. GIUS-4-251/D-81: Frasnian upper Sitkówka Beds, Jaźwica (set H). □F-H. *Radiatrypa* cf. *multicostellata* (Kottłowski 1951), dorsal, lateral, and anterior views. GIUS 4-178/1, Givetian *Stringocephalus* Beds: Łągów. □I. *Variatrypa* aff. *clarkei* (Warren 1944), ventral view. GIUS 4-254/A-1: Frasnian upper Sitkówka Beds, Jaźwica (set I). All × 2.

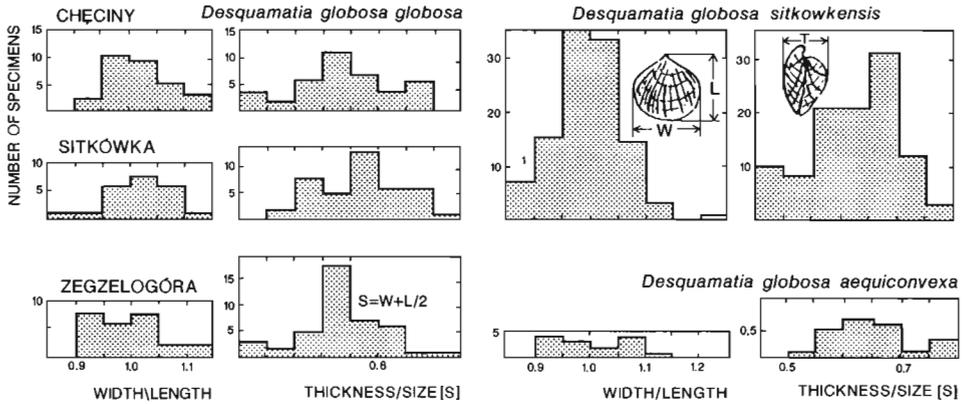


Fig. 6. Variability of principal morphological indices for subspecies of *Desquamatia globosa* from different sites.

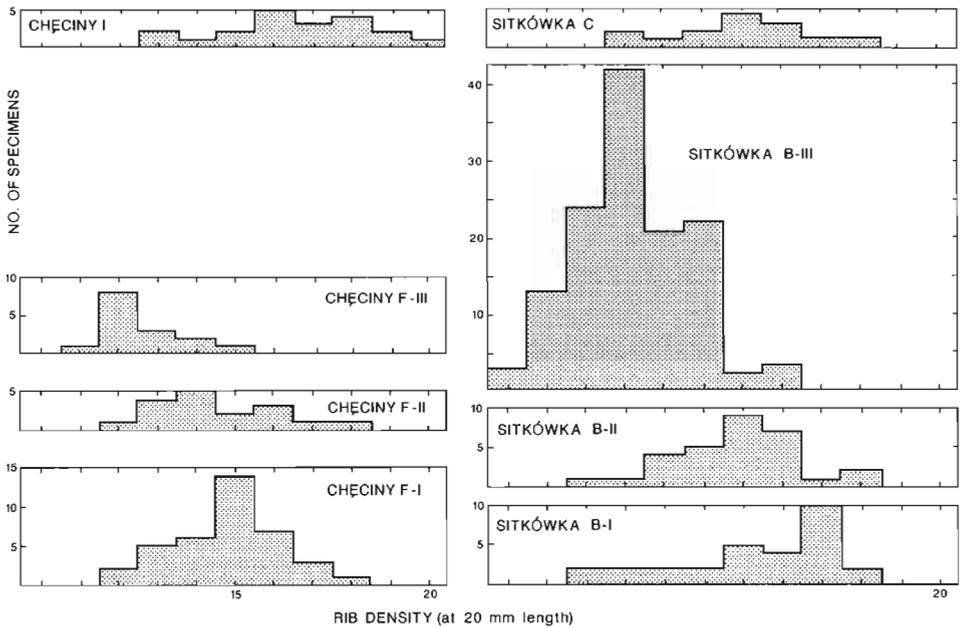


Fig. 7. Stratigraphic sequence of rib density for *Desquamatia globosa* in Checiny (only nominative subspecies: see Racki & Baliński 1981) and Sitkówka sections, given for particular shell beds (corresponding to lithologic sets; B-I – *D. g. globosa*, B-II – *D. g. aequiconvexa*, B-III – *D. g. sitkowkensis*, C – *D. aff. macroumbonata*). Note apparent trend, not expressed by other indices (see Fig. 6).

to Sitkówka-Kostrzewa (set B₁). *Desquamatia globosa sitkowkensis* subsp. n. (Figs 6-7, 9, 14J; for description see p. 324) is known from the Givetian to Frasnian passage strata at Sitkówka-Kostrzewa (sets B₂-?C) only.

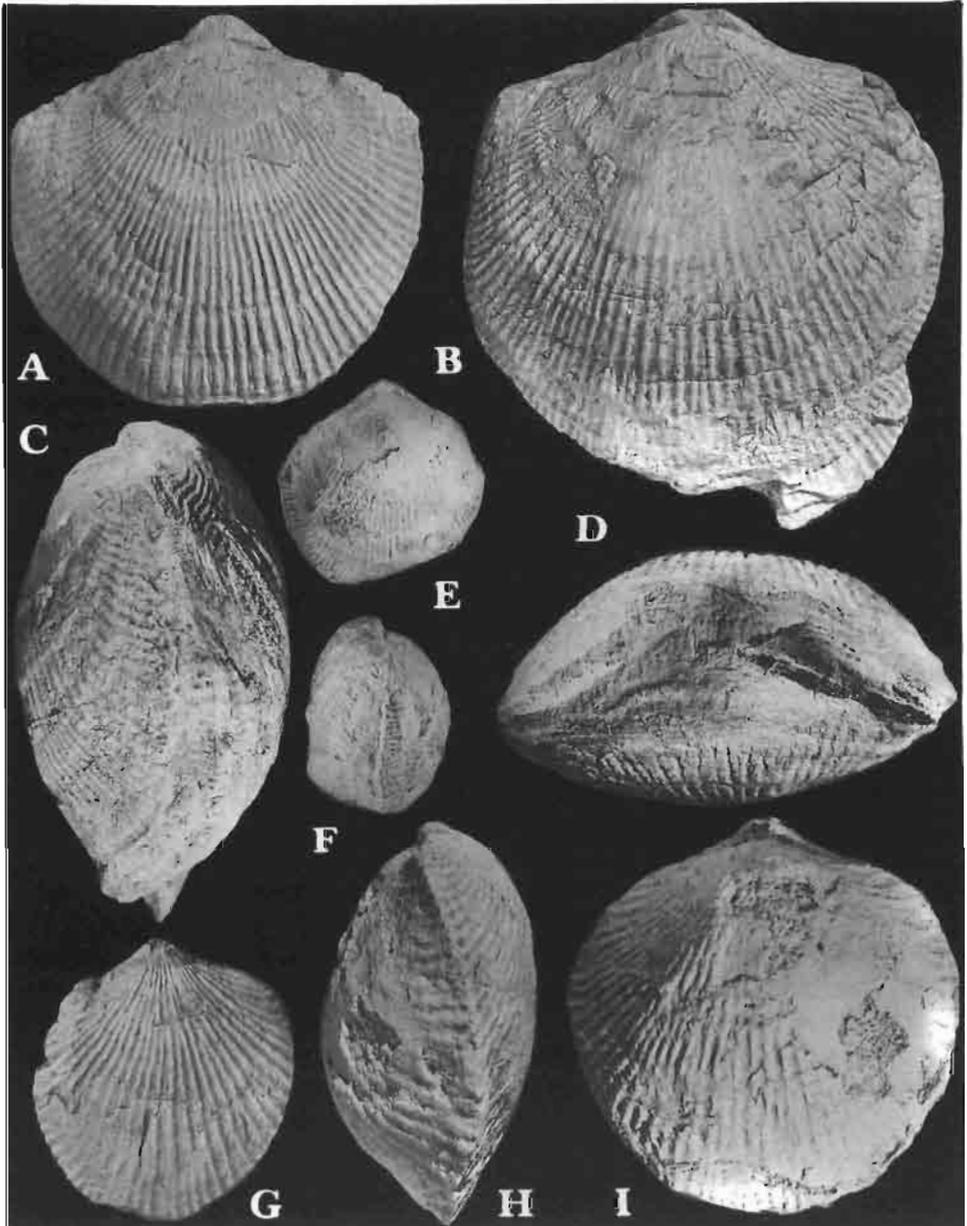


Fig. 8. A-F. *Desquamatia globosa aequiconvexa* subsp. n., different-size shells in dorsal, lateral and anterior views; B-D - holotype GIUS 4-238a/D-1 (L=29.4 mm, W=29.0 mm, T=16.2 mm, Tb=8 mm, h=5 mm, z/10=18, z/20=11); E-F - specimen transitional to *D. globosa globosa*, GIUS 4-238a/D-2 (A), D-3 (E-F); Givetian Chęciny Beds, Sitkówka-Kostrzewa (set B₁, bed B-II). G-I. *Desquamatia* sp. A, dorsal and lateral views, GIUS 4-221/D-1 (G), GIUS 4-229/D-1 (H-I); Givetian lower Sitkówka (G) and Chęciny (H-I) Beds, Biczka (set B; G), Sosnówka (set B; H-I). All $\times 2$ except for E-F (natural size).

***Desquamatia* aff. *macroumbonata* Racki 1985** (Figs 7, 10C-D).— Silicified specimens from the basal Sitkówka Beds of Sitkówka-Kostrzewa (set C) are of small size, equibiconvex to dorsibiconvex, elongate-subovate, finely ribbed with prominent, erected beak. Weakly uniplicate anterior commissure clearly occupy a transitional position (cf. Racki 1985: p. 67) between *D. globosa* and *D. macroumbonata* Racki 1985 (Fig. 10A-B). The latter species displays a still protruding ventral beak combined with small shell size, even biconvexity or dorsibiconvexity, and rectimarginate anterior margin. Sobolev (1909: p. 487) described these atrypids under the name *Atrypa desquamata* var. *alticola* Frech 1891.

The specific assignment is equivocal because of inadequate material available (viz. 6 complete and 12 damaged shells, 5 fragments), and obscure relationships of other large-beaked, poorly known species of *Desquamatia*. Somewhat similar, although more circular forms were reported from the Early Frasnian of Canada as '*Atrypa* sp. 468' by Maurin & Raash (1972).

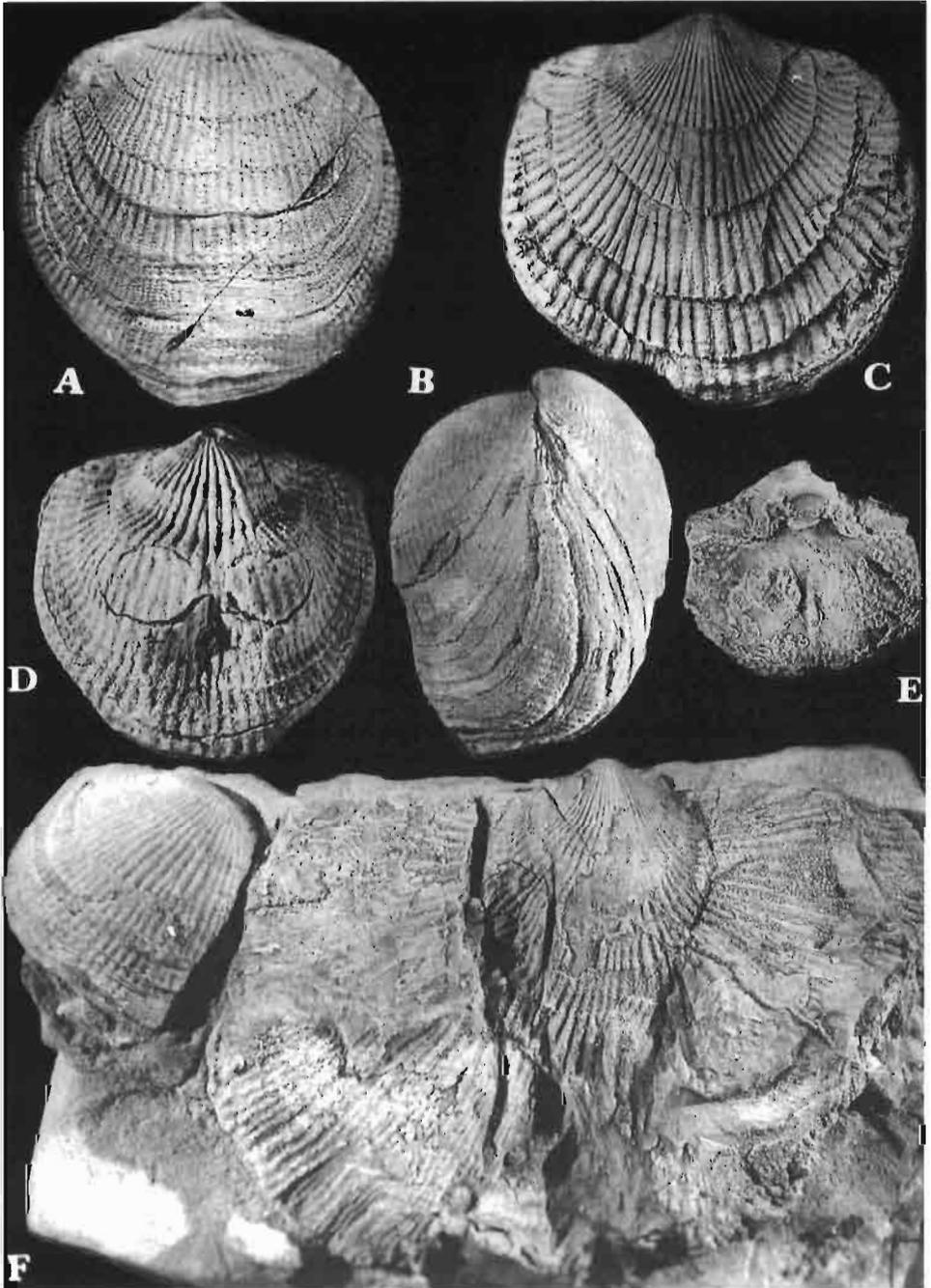
***Desquamatia*(?) sp. A** (Fig. 8G-I).— The flattened, nearly equally biconvex specimens resemble *D. globosa aequiconvexa* subsp. n., but they have a more suberect ventral beak, widely separated radiating costae and infrequent (?subdued) growth lamellae. In this last aspect the shells are close to those of *Variatrypa* and *Desatrypa*, but the scarce material (5 whole and 5 almost complete shells, 10 fragments) precludes more precise determination. The species occurs in the Late Givetian lower Sitkówka and Chęciny Beds at Bilcza (set B), Zegzelogóra, and Sosnówka (set B).

***Variatrypa* aff. *clarkei* (Warren 1944)**.— Atrypids with weak development of growth lines are markedly typical of Frasnian strata under study. Widespread, but everywhere sparse forms (Fig. 5I), showing subcircular to transversely-oval outline, moderately high equibiconvex to dorsibiconvex profile and costae varying in thickness ($z/20$ is 13-18) are less inflated and more thickly ribbed than the typical *V. clarkei* from the latest Givetian and Early Frasnian (Waterways Formation) of Canada (Copper 1978; Norris & Uyeno 1983). *Atrypa kadzielniae* Gürich 1896 from Kadzielnia probably also belongs to *Variatrypa*, and not, as proposed by Nalivkin (1930), to *Iowatrypa* (thus unknown in the Kadzielnia quarry).

***Radiatrypa* cf. *multicostellata* (Kottlowski 1951)**.— A few exceedingly finely costate Givetian specimens from Łągów (Fig. 5F-H) resemble *R. multicostellata* from the Frasnian of North America (McLaren *et al.* 1962; Johnson *et al.* 1980a), but are more flattened, weakly uniplicate, and slightly more delicately ornamented.

***Iowatrypa timanica* (Markovsky 1939)** (Figs 11A-F, 12, 13D-E).— Above 80 complete shells and 100 damaged shells and valves, commonly deformed, from Chęciny vary in convexity. The generically diagnostic

Fig. 9. *Desquamatia globosa sitkownikensis* subsp. n., three shells in dorsal, lateral and ventral views (A-D); note variable ribbing; A-B - holotype GIUS 4-238b/D-8 (L=25.1 mm, W=25.0 mm, T=15.4 mm, Tb=9.5 mm, h = 2 mm, $z/10=17$, $z/20=12$); internal mold of posterior part



in dorsal view (E); prominently frilled shell in ventral view, and non-frilled specimen in oblique-dorsal orientation (F); GIUS 4-238b/D-10 (C), D-130 (D), D-101 (E), D-1a, b (F); Givetian to Frasnian transition, Chęciny Beds, Sitkówka-Kostrzewa (set B₂). All × 2.

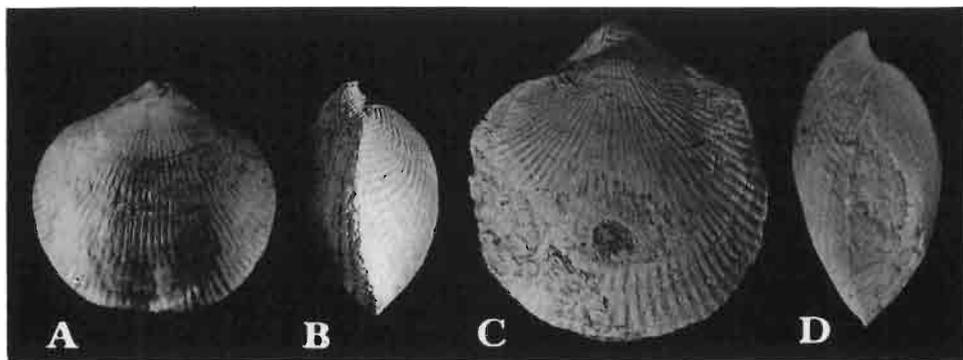


Fig. 10. Early Frasnian atrypids of the basal Sitówka Beds. □A-B. *Desquamatia macroumbonata* Racki 1985, dorsal and lateral views, GIUS 4-251/D-1; Jaźwica (set H). □C-D. *Desquamatia* aff. *macroumbonata* Racki 1985, dorsal and lateral views, GIUS 4-239/D-132; Sitkówka-Kostrzewa (set C, uppermost part). All $\times 2$.

ventribiconvexity occurs rarely, similarly as in *I. timanica* from Kuznetsk Basin (Alekseeva 1962), as well as in *Desquamatia macroumbonata* (see Racki 1985). Thus, the taxonomic value of this feature is somewhat questionable. Variable are also the shell outline (Fig. 8) and appearance of the anterior fold, whereas relatively constant values have been noted for ribbing.

Small-sized specimens from the Chęciny Beds with finely-imbricated ornamentation well agree with *I. timanica* from the Russian Platform, in particular with forms figured by Lyashenko (1959, 1973). The Asiatic variant of this species displays a more circular outline and more wide ventral beak (Alekseeva 1962). Conspecific with the Holy Cross Mountains species seems to be '*Anatrypa kadzielniae*' sensu Nalivkin (*non* Gürich), marked only by more widely spaced concentric lamellae (Alekseeva 1962).

In the Holy Cross Mountains the species is limited to the Early Frasnian Chęciny Beds at Góra Zamkowa (set J) and Rzepka. Reported from the East European Platform, Urals, and Kuzbass; also from the Early Frasnian (Sargaievo horizon).

***Spinatrypina comitata* Copper 1967** (Figs 11G-I, 14O).— Six complete and above 30 incomplete shells, and ca. 50 fragments (chiefly exfoliated) include a coarse costate, rarely strongly lamellose, rectimarginate variety typical of the Sosnówka-Zegzelogóra outcrops. The morphotype from Góra Zamkowa is finer-ribbed and has a marked dorsal fold. Similar, although larger-sized and dorsibiconvex specimens, with deflected anterior commissure, determined to be *Spinatrypina* sp. A, are scarcely represented in the Sitkówka atrypid succession (set C). Ventribiconvex and elongated specimens from Chęciny can be confidently identified as *S. comitata* Copper 1967, although they are close in the main shell characteristics also to Australian *S. (S.) prideri nurungunia* Grey 1978. The more coarsely ornamented variant resembles *S. nana* (Khal'fin 1938) from the Givetian of the Kuznetsk Basin (Alekseeva 1962; Rzhonsnitskaja 1975). The early

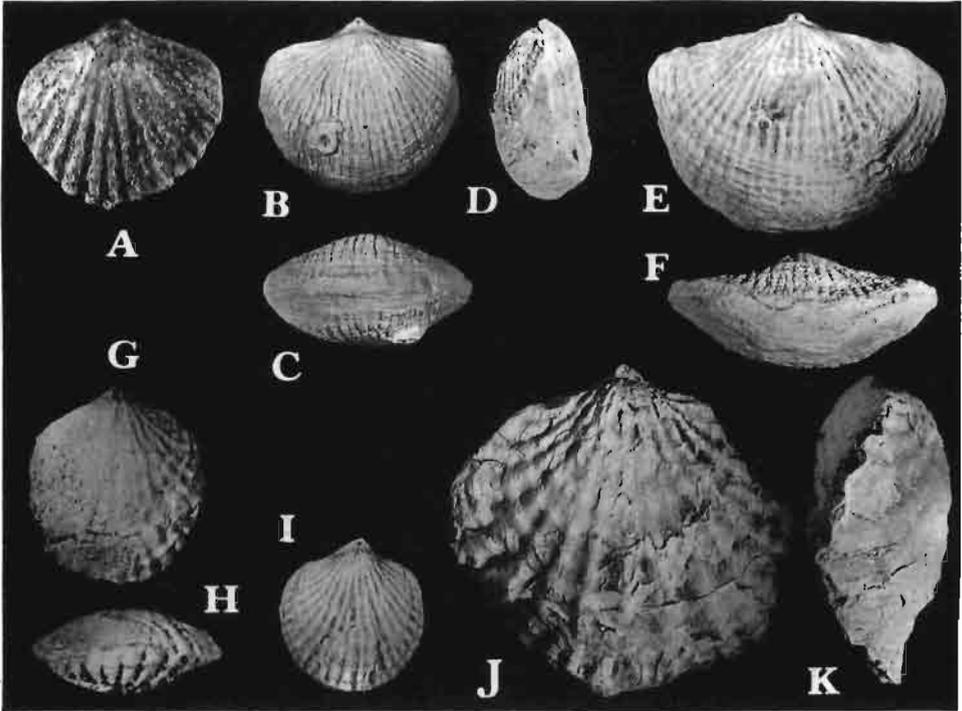


Fig. 11. □A-F. *Iowatrypa timanica* (Markovsky 1939), dorsal, anterior and lateral views; GIUS 4-246/20 (A), 16 (B-D), GIUS 4-245/A-1 (E-F); Frasnian Chęciny Beds, Rzepka (A-D), Góra Zamkowa (eastern outcrop, set I; E-F). □G-I. *Spinatrypina comitata* Copper 1967, dorsal and anterior views, GIUS 4-230/A-1 (G-H), GIUS 4-227/S-1 (I); Givetian Chęciny Beds, Zegzelogóra (set B; G-H), Góra Zamkowa (set C; I). □J-K. *Spinatrypa* cf. *semilukiana* Lyashenko 1959, dorsal and lateral views, GIUS 2-230/A-1; Givetian Chęciny Beds, Zegzelogóra (set A). All $\times 2$.

Frasnian *S. comitata* from the Kadzielnia Member is more finely costate, and exhibits less developed umbonal lateral cavities and delicate hinge plates (see Biernat 1971), as compared to the Givetian forms.

S. comitata occurs in the Late Givetian (lower Chęciny and Sitkówka Beds): Góra Zamkowa (set C), Sosnowka (set B), Zegzelogóra (sets ?A-B), Biczka (set B), possibly also Jazwica (sets C-D) and Stokowka (sets C, E). In the Rhenish Slate Mountains it is reported from the earliest Frasnian (Refrath Formation; Copper 1967b).

The distinction between *Spinatrypa* and *Spinatrypina* is somewhat ambiguous (Roberts 1971; Johnson & Flory 1972) because of variable development of area and ornamentation, frequently obscured by preservation; the diagnostic spines might be broken during the life of the animal (Stainbrook 1938; Frost & Langenheim 1966). Consequently, the generic position of some species changes from author to author, as the case with e.g. *Spinatrypa wotanica* Struve 1955 (see Copper 1967c; Struve & Mohanti 1970) and *Spinatrypa prideri* Veevers 1959 (see Veevers 1959b; Roberts 1971; Grey 1978).

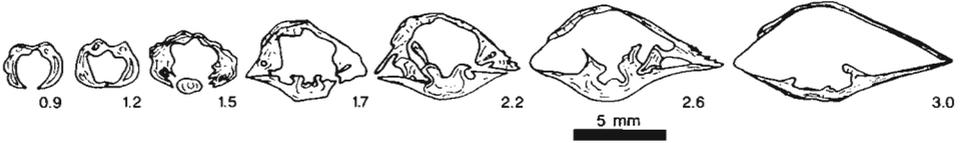


Fig. 12. Serial sections of *Iowatrypa timanica* from Góra Zamkowa, GIUS 4-244/A-8; Frasnian Chęciny Beds (set I).

***Spinatrypina ex gr. tubaecostata* (Paeckelmann 1913)** (Figs 13, 14B-C, K-N).— Twenty complete and 30 damaged examined shells show marked variation in size of costae ($z/10$ ranges from 7 to 12). The small-sized specimens from Jaźwica frequently exhibit gerontic features (Fig. 14B-C), and are more rounded and ventribiconvex than the Sitkówka variants. The main distinction between *S. ex gr. tubaecostata* and the mostly stratigraphically older *S. comitata* includes the more circular outline, thicker costae and invariably present dorsal fold. *S. tubaecostata* (Paeckelmann 1913) was restricted by Copper (1967b) to the atrypid form of the Rhenish Givetian to Frasnian passage beds (Struve 1982) which is larger, wider more flattened than this from the Holy Cross Mountains. The specimens examined resemble the most the Russian Frasnian atrypids assigned to *S. tubaecostata* group by Lyashenko (1959), as also to *S. communis* Lyashenko 1969 from the Givetian of Russia and *S. (S.)* sp. from the basal Frasnian of Dębnik near Cracow (Baliński 1979).

The atrypid species occurs in the Early and maybe Middle Frasnian Sitkówka Beds (Jaźwica; set H; Sitkówka-Kostrzewa, set C; Zelejowa, set A; possibly also Kowala, see Biernat 1969, Sowie Górki, set G, and Sitkówka-Kowala, set C).

***Spinatrypina robusta* Copper 1967** (Figs 13, 14H-I, 15B-H).— The distinctive late Givetian, mass occurring species is represented by 40 more or less complete shells and above 70 fragments, collected from the topmost *Stringocephalus* Beds to basal Sitkówka Beds at Poślowice (sets A-C), Marzysz and Trzemoszna. It was also found at Górno (Laskowa Góra Beds), Wietrznia (set A), and in the Iwaniska-Piskrzyn section (see Ozonkova 1961). Shell shape, dorsal deflection of anterior commissure and rib size exhibit a rather high range of variability (Fig. 13). Some globose specimens, often with asymmetric beak part, have been largely collected at Trzemoszna. This representative of *Spinatrypina* is assigned to *S. robusta*, described from the earliest Frasnian Refrath Formation, because of relatively advanced shell convexity and lack of internal umbonal cavities. The only difference is a finer costation of the Holy Cross Mountains specimens (Z_{AP} is 10-11 and 8-10 in Polish and German forms, respectively). In the collection there are more rectangular and flat specimens transitional to *S. explanata* (Schlotheim 1820), as well as a thick-ribbed morphotype close to *S. tubaecostata* sensu Copper (1967b). Some smaller specimens show notable resemblance to *Spinatrypina* cf. *explanata* from the Early Frasnian of Boulonnais (Godefroid 1988). Another comparable

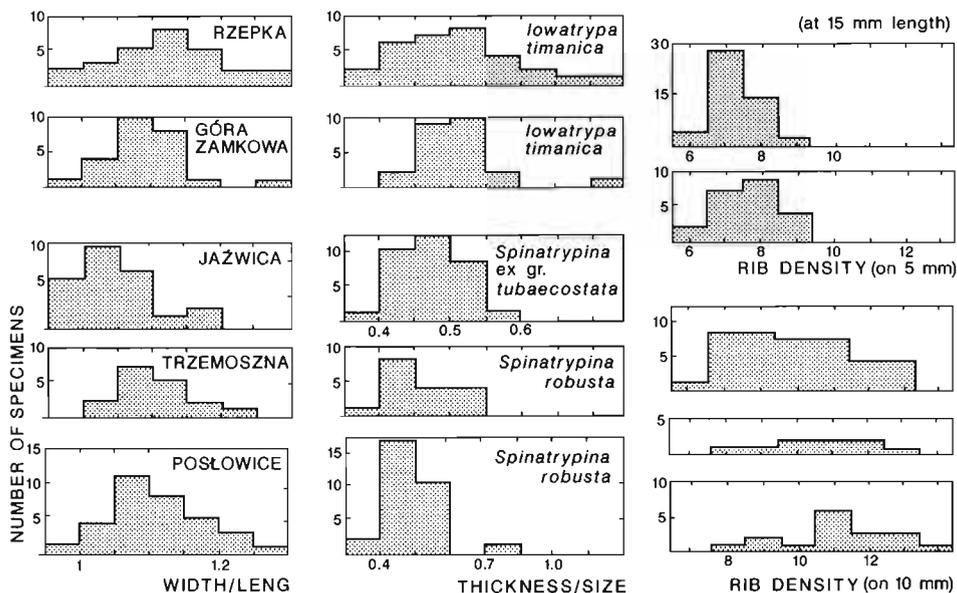


Fig. 13. Frequency distribution of principal shell indices for species of *Spinatrypina* (lower part) and *lowatrypa timanica* (upper part).

species is *Spinatrypa prideri larga* Roberts 1971 from the Frasnian of Australia displaying merely more incurved ventral beak.

***Athyris ex gr. A. concentrica* (von Buch 1834)** (Figs 15A, 16A-E, H).— The material contains 20 complete and 10 damaged shells, 20 fragments, usually exfoliated and weathered. They have been gathered from the topmost *Stringocephalus* Beds to basal Sitkówka Beds at Posłowice (set C). There are also loose specimens, without precisely known stratigraphic position from Marzysz, Trzemoszna and Bilcza. Juvenile shells of athyrids are known from the Jaźwica Member at such sites as Jaźwica, Góra Sołtysia, Góra Zamkowa. The collection from Posłowice shows how the species is variable in shell convexity, development of tongue, beak shape, dental plates, and of dorsal median interior. The lack of prominent concentric lamellae and invariably well developed, rectangular to trapezoidal tongue allows to separate the studied form from populations of *Athyris concentrica* of the type (Eifel) area (Schnur 1853; Kayser 1871), as well as from the Eifelian/Givetian passage of the Skały Beds (Biernat 1966) alike to the coeval Moravian species *A. mollizonata* Ficner & Havlíček 1978 (Ficner & Havlíček 1978: Pl. 12: 4-6). The Holy Cross Mountains species exhibits far more intensive deflection of the anterior commissure. As pointed out by Grunt (1980: p. 54), '*Athyris concentrica*' is a catch-name for many Devonian athyridids essentially unknown internally; thus an adequate assessment awaits the revision of the group.

***Cyrtospirifer ex gr. aperturatus* (Schlotheim 1822).**— The cyrtospiriferids are scarcely represented in the collection studied, although they

were encountered in several localities (see Fig. 16F-G). For example, large Late Givetian forms from Stokówka (set C) seem comparable with the tenticuloid varieties of *Cyrtospirifer schelonicus* Nalivkin 1941 from the Frasnian of Russia (Nalivkin 1947; Krylova 1955; Lyashenko 1959) and the Kuznetsk Basin (Rzhonsnitskaja 1952). The former have a generally shallower sulcus and lower fold, and no alate extensions of cardinal margin have been observed (Fig. 17G, I, K). Smaller form from Chęciny (set A₂) is close to *Cyrtospirifer aperturatus* (Schlothheim 1822) *sensu* Paeckelmann 1942, described from the Middle to Late Devonian transition ('Plattenkalk') of the Rhenish area (see also Struve 1982).

***Tenticospirifer lagoviensis* (Gürich 1896)** (Figs 17H-J, 18, 19D-K).— For redescription see p. 325. The species is established in the Late Givetian *Tenticospirifer* Level being an equivalent of Jaźwica Member, and overlying strata of Łągów (Ferańska 1961), Krępa Dolna (Lenkiewicz 1981), and several other sites in the eastern part of the Holy Cross Mountains (Samsonowicz 1917; Kotański 1959), including Janczyce 1 borehole.

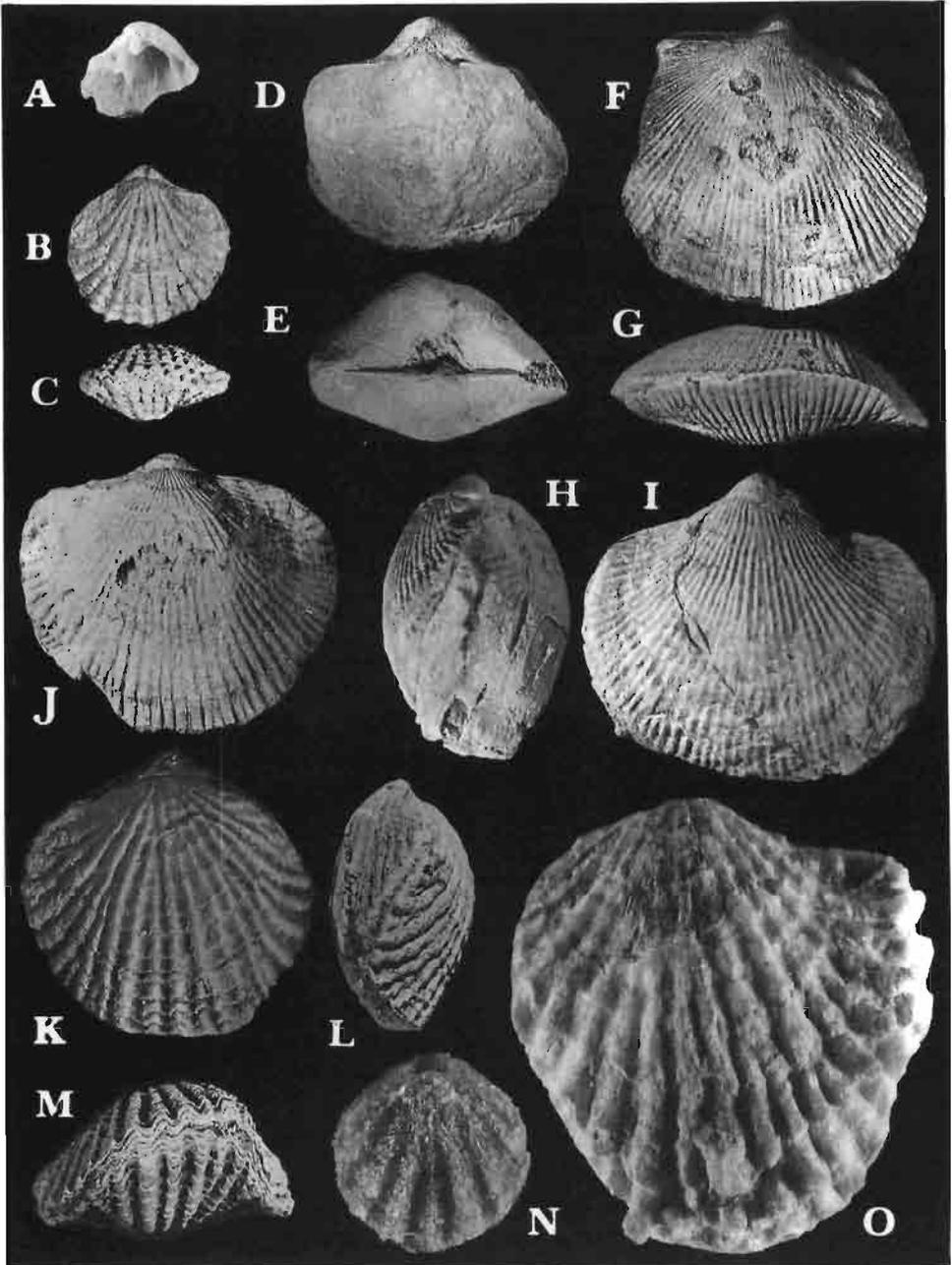
***Tenticospirifer cf. utahensis* (Meek 1876)** (Fig. 17A, C-F, L).— Late Givetian lower Chęciny and Sitkówka Beds of Zegzelogóra, Sosnówka (set B) and Sitkówka-Kostrzewa (set C) yield 3 almost complete shells and 3 dorsal valves. These sparsely represented tenticospirifers with bifurcated median costae are half of size and less coarsely ribbed in comparison with *T. utahensis* from the Frasnian of Ardennes (Vandercammen 1959).

***Rhynchospirifer hians* (von Buch 1836)** (Figs 23D-F, M-N, 24E).— Included to *Ilmenia* by Baliński (1973), the species was reassigned to *Rhynchospirifer*. The concept of genus *Ilmenia* Nalivkin 1941 remains disputable due to poor knowledge of the type species *I. altovae* Nalivkin 1941 (see also Krylova 1955), and in consequence varies from author to author (Dürkoop 1970; Ficner & Havlíček 1978; Johnson & Trojan 1982). *R. hians* occurs in the Middle Givetian *Stringocephalus* Beds (Jurkowice-Budy, set E; Baliński 1973) and Dziewki Limestone of the Silesia-Cracow Region (set D). It characterizes the Rhenish Eifelian to Givetian transition (Paulus 1957; Struve 1982).

***Ilmenia(?) elatior* (Gürich 1896)** (Figs 21A, 22, 23A-C, G-I, 24C-D, F-G). For redescription see p. 326. The species is known from a late part of the Middle Givetian (upper *Stringocephalus* Beds; Ambocoeliid Level) at Góra Zamkowa, Góra Łgawa (set A₁), Góra Sołtysia, Bilcza hills, and maybe Ołowianka (set C).

***Crurispina 'inflata'* (Schnur 1853)** (Figs 17B, 19A-B, 20D, 21B-C, 22, 23J-L, 24A-B, H-I).— Above 200 complete and 400 damaged, chiefly

Fig. 14. □A. *Warrenella(?)* sp., interior of fragmented ventral valve with distinctive dental plates, GIUS 4-238b/O-1; Givetian to Frasnian transition Chęciny Beds, Sitkówka-Kostrzewa (set B₂). □B-C, K-N. *Spinatrypina* aff. *tubaecostata* (Paeckelmann 1913), different size shells in dorsal, anterior and lateral views, GIUS 4-251/S-1 (B-C), GIUS 4-239/S-14 (K-M), S-18 (N); Frasnian upper Sitkówka Beds, Jaźwica (set H;B-C), Sitkówka-Kostrzewa (set C; K-N). □D-E. *Warrenella* cf. *euryglossa* (Schnur 1853), shell in dorsal and posterior views, GIUS 4-239/O-1; Frasnian upper Sitkówka Beds, Sitkówka (set C). □F-G. *Variatrypa* cf. *ajugata* (Copper 1965),



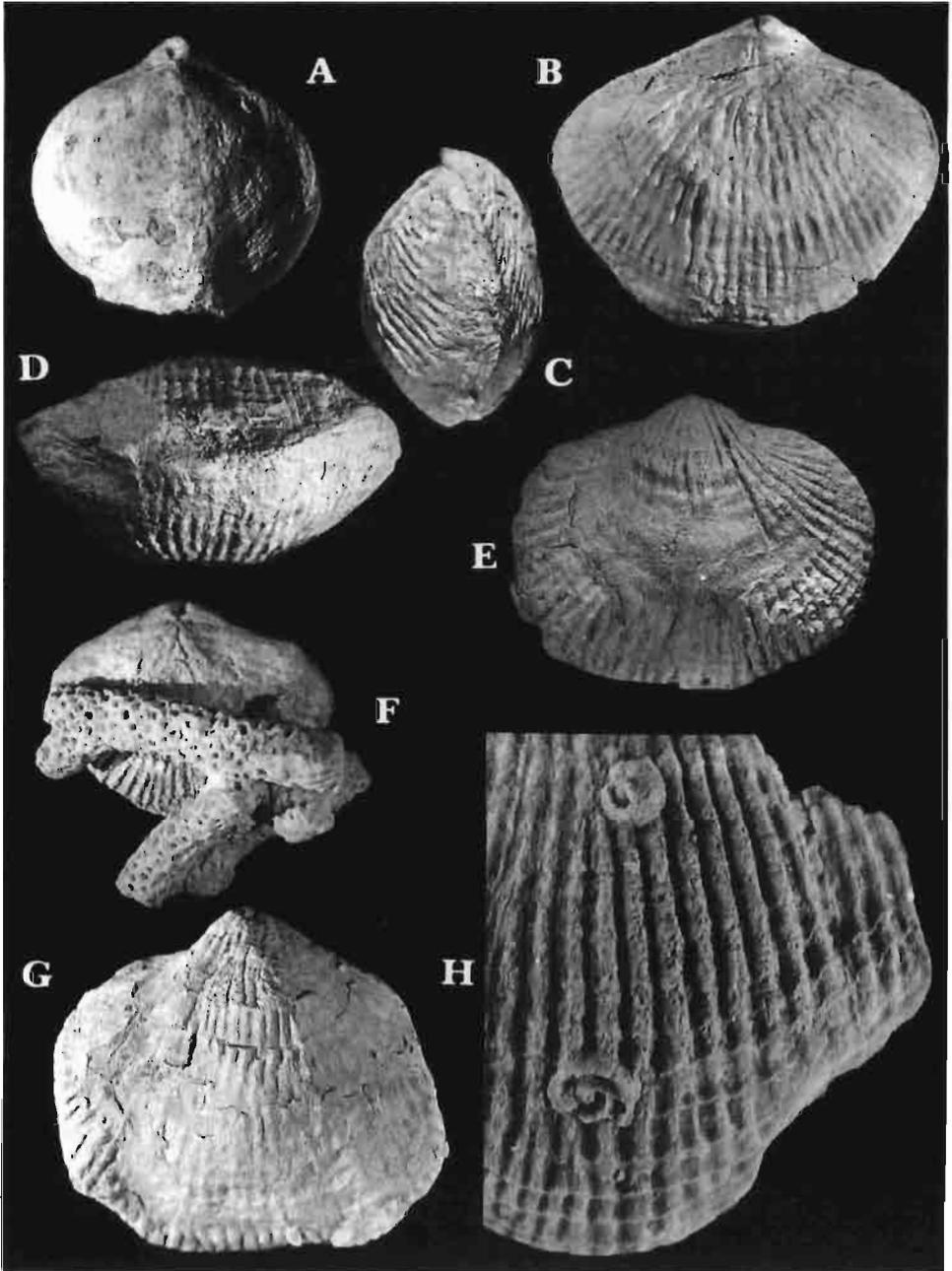
damaged shell in dorsal and anterior views, GIUS 4-252/A-1; Frasnian upper Sitkówka Beds, Sitkówka-Kowala (set C). □H-I. *Spinatrypina robusta* Copper 1967, ventral and lateral views, GIUS 4-220/S-1; Givetian lower Sitkówka Beds, Posłowice (set C). □J. *Desquamatia globosa sitkowkensis* subsp. n., wide shell variety in dorsal view, GIUS 4-238b/D-13; Givetian to Frasnian transition Chęciny Beds, Sitkówka-Kostrzewa (set B₂). □O. *Spinatrypina comitata* Copper 1967, shell with preserved spines in dorsal view, GIUS 4-221/S-1; Givetian lower Sitkówka Beds, Bilcza (set B). All × 2 except for N and O that are × 10.

juvenile shells, and more than 200 fragmentary specimens exhibits similar range of variability as *Ilmenia(?) elatior*. The specimens are grouped into two distinctive variants (Fig. 22): (A) small-sized (below 10 mm long), circular, frequently globose shells with rectimarginate anterior commissure and only uncommonly exposed 'microspines' (see *Spirifer* aff. *hians* sensu Sobolev 1909: Pl. 5: 8), and (B) significantly larger (15-20 mm in length), transversely outlined and less inflated shells with variously expressed sulcus and well visible secondary ornament of papillae and striae. Inclusion of the two so distinct varieties in a single species is based on inferred ecologic gradients between coeval populations. Morphotype A differs from the Eifelian *Spirifer inflatus* Schnur 1853 *sensu stricto* in having a more massive and erect ventral beak, and weaker median sulcus (see also Sobolev 1909: p. 470), and this seems also true for the other forms assigned to this species, usually classified as *Crurithyris* (e.g. Biernat 1966; Ficner & Havliček 1978). Some Devonian *Crurithyris*-like ambocoeliids from New York were transferred to the new genus *Crurispina* by Goldman & Mitchell (1990). The Holy Cross Mountains species deserves this placement even if they have a more convex shell and only rarely develop a sulcus. Possibly this is the same case with almost spherical *C. jurkowicensis* Baliński 1973.

Because the type collection of Schnur has been lost (Jux & Strauch 1965; Struve, letter communication 1984), the limits of variability in the type population of *S. inflatus* remain up to now unrecognized. German authors (Packelmann 1913; Leidhold 1928) treat the species very broadly. The morphotype B resembles *I.(?) elatior* but it can be distinguished by the general lack of dental plates and more flattened shell. Such forms, together with *S. inflatus* (Rzhonsnitskaja 1952; Bublitchenko 1974), have been usually attributed to *Emanuella*, which displays, however, primarily concentric spinose ornamentation known in the type species *E. takwanensis* (Kayser 1879) (Veevers 1959a) and elevated cardinal process (Goldman & Mitchell 1990). Nevertheless, knowledge of the ornament origin is a prerequisite to any reliable comparison with such Middle Devonian 'emanuellids' as *E. pseudopachyrincha* (Tschernyshev 1887) (Tjazheva 1962; Breivel & Breivel 1972), *E. samsonowiczi* Kelus 1939 or *E. alveosimilis* Dürkoop 1970.

This widely distributed, Eifelian to Frasnian species (Vandercammen 1956) occurs in the later Givetian topmost *Stringocephalus* Beds to basal Sitkówka Beds. Morphotype A has been found at Jaźwica (sets A-C), Góra Zamkowa (set A₂), Stokówka (set B), Marzysz, Szczecno-1 borehole (set B), Zbrza (sets A-B; Kucia 1987), with some question at Zegzelogóra, as well as in the topmost Dziewki Limestone (set E), and possibly the Dębnik Limestone of the Silesia-Cracow region. Morphotype B characterizes only Posłowice (sets A-C) and Trzemoszna sites.

Fig. 15. □A. *Athyris* ex gr. *concentrica* (von Buch 1834), dorsal view, GIUS 4-182/1; Givetian ?lower Sitkówka Beds, Bilcza (?set A). □B-H. *Spinatrypina robusta* Copper 1967, dorsal, ven-



tral. lateral and anterior views (B-G), note asymmetry of umbonal part; details of sculpture, with attached microcornids (H). GIUS 4-220/S-2 (B-D), S-3 (E), S-21 (F), S-30 (H), GIUS 4-219/S-1 (G); Givetian lower Sitkówka Beds, Posłowice (set C: B-F, H) and Trzemoszna (G). All $\times 2$ except for H that is $\times 5$.

***Rensselandia cf. circularis* Holzapfel 1908** (Fig. 25F-I).— Fragmentary specimens from the coquinas of Jurkowice-Budy (basal *Stringocephalus* Beds; set A) exhibit suboval, weakly and subequally biconvex shells with not especially prominent beak. They possess discrete hinge plates and recall larger-sized *Rensselandia circularis* Holzapfel 1908 (perhaps *Newberria*; Struve 1982) from the Rhenish and Uralian Givetian (Döring 1919; Torley 1934; Tjazheva 1962). *R. gregaria* Ficner & Havlíček 1978 from the Eifelian-Givetian transition of Moravia displays a more transversely elongate shell. *R. cf. circularis* from the same stratigraphic interval of the Bodzentyn Syncline can be distinguished by the projecting acute ventral beak (Biernat 1966); the species was listed by Łobanowski (1981) from the Emsian(!) of the area. A more large-sized and subcircular *R. gibbosa* Cloud 1942 was described by Baliński (1973) from the younger strata of Jurkowice-Budy.

***Stringocephalus 'burtini* Defrance 1825'**.— The species has been cited from several sites as a guide species (Gürich 1896; Kotański 1959: p. 272), but was described in detail only from Jurkowice-Budy (Baliński 1973) and Brudzowice-Dziewki (Baliński 1971). Filonowicz (1967, 1973) reported *S. aff. burtini* from Czarnów (set A) which differs from the typical German species as described by Cloud (1942) in being more extended along the cardinal margin and therefore subtrigonally outlined. Internally, the Czarnów specimens show markedly triangular hinge plates (Fig. 26). Distinctly transversely widened specimens, known from Jurkowice-Budy (Fig. 25E; Baliński 1973: Pl. 12: 4) may represent another species (see stringocephalid revision in Struve 1992). One moderate-sized complete stringocephalid shell, having both valves sulcate and thus close to *Parastringocephalus parasulcatus beyrichi* Struve 1982 (Fig. 25A-B), was found in the Dziewki Limestone (cf. also Struve 1992: pp. 518-519). Fragments of large shells and their moulds, as well as singular thick valves with high median septum were found in several sections of the Holy Cross Mountains (Ołowianka, set B; Sowie Górki, sets A-B; Laskowa, set A₁), and in the Dębniak Anticline of the Cracow area (Siedlec Limestone; Łaptaś 1979).

Description of new and poorly known species

Abbreviations.— L – shell length; W – shell width; T – shell thickness; S – shell size $(W+L/2)$; WI – width index (W/L) ; TI – thickness index (T/S) ; W_z – width of cardinal margin; Tb – convexity of brachial valve; E.I. – equiconvexity index (Tb/T) ; h – height of sinus; z, z-5, z-10 – density of radial sculpture elements on 1, 5 and 10 mm, respectively; z/10; z/15 and z/20 – density of radial sculpture elements in distance of 10, 15 and 20 mm from ventral umbo, respectively; Z_{AP} – density of radial sculpture elements along anterior commissure; K-5, K-1 density of concentric sculpture elements on 5 and 1 mm, respectively; ns – number of ribs in sinus.

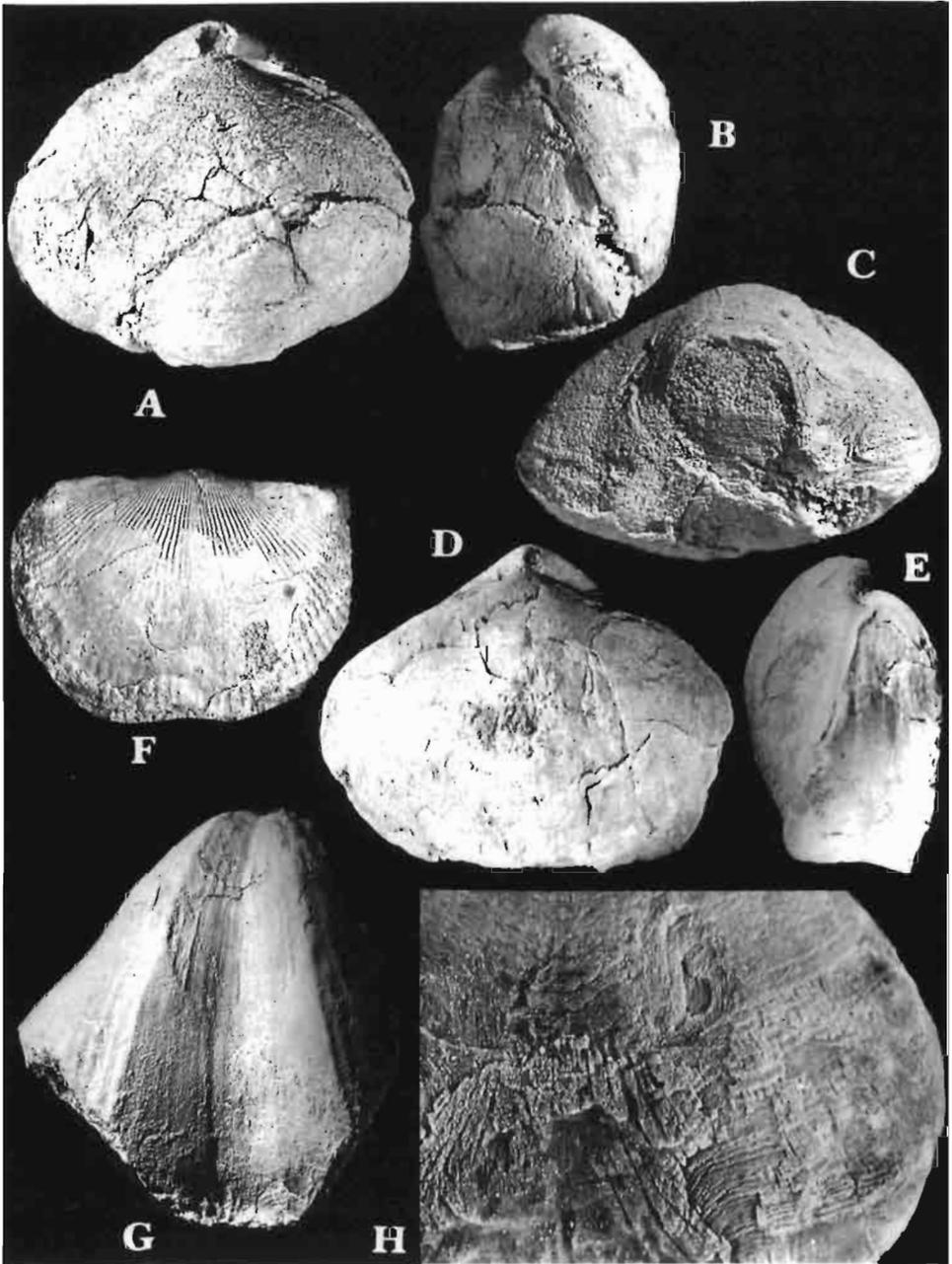


Fig. 16. □A-E, H. *Athyris* ex gr. *concentrica* (von Buch 1834), dorsal, lateral and anterior views (A-E), and detailed view of concentric/radial sculpture (H), GIUS 4-215/A-1 (A-C), GIUS 4-220/A-1 (D-E), A-10 (H); Givetian lower Sitkówka Beds, Marzysz (A-C) and Posłowice (set C; D-E, H). □G-H. *Cyrtospirifer*(?) sp., dorsal valve (F) and incomplete shell in anterior view (G); GIUS 4-242/B-1 (F), GIUS 4-230/O-9 (G); Frasnian upper Sitkówka Beds, Jaworznia (F) and Givetian Chęciny Beds, Zegzelogóra (set B; G). All $\times 2$ except for H that is $\times 5$.

Family Productellidae Schuchert & La Vene 1929

Genus *Praewaagenoconcha* Sokolskaja 1948

Praewaagenoconcha(?) *sobolevi* sp. n.

Figs 1C-F, 2A-D, E, H-I.

Holotype: GIUS-4 217 Ps/P-1; Fig. 2A-B.

Type horizon and locality: Posłowice facies of the Jazwica Member, Kowala Formation, Late Givetian; Posłowice, abandoned pit on a hill S of the Kielce suburb, Poland.

Derivation of name: After Dymitr N. Sobolev, the prominent Russian investigator of the Holy Cross Mountains in the beginning of the century.

Material.— Ten almost complete isolated shells; 20 ventral and 7 brachial valves embedded in rock, above 40 different fragments.

Diagnosis.— Large-sized productellids with transversely elongated shell, well developed ventral beak and ornamentation with more or less regular concentric rugae, mostly bearing short spine ridges placed alternately (quincuncial pattern); the median ridge is rarely traceable.

Description.— Shells large (up to 35 mm in width). The hinge line is straight, of slightly less than the maximum width, the anterior half of the shell is evenly rounded.

The ventral valve displays a prominent beak that overhangs the linear area and a row of obliquely directed spines along the hinge. The dorsal valve is gently and evenly concave.

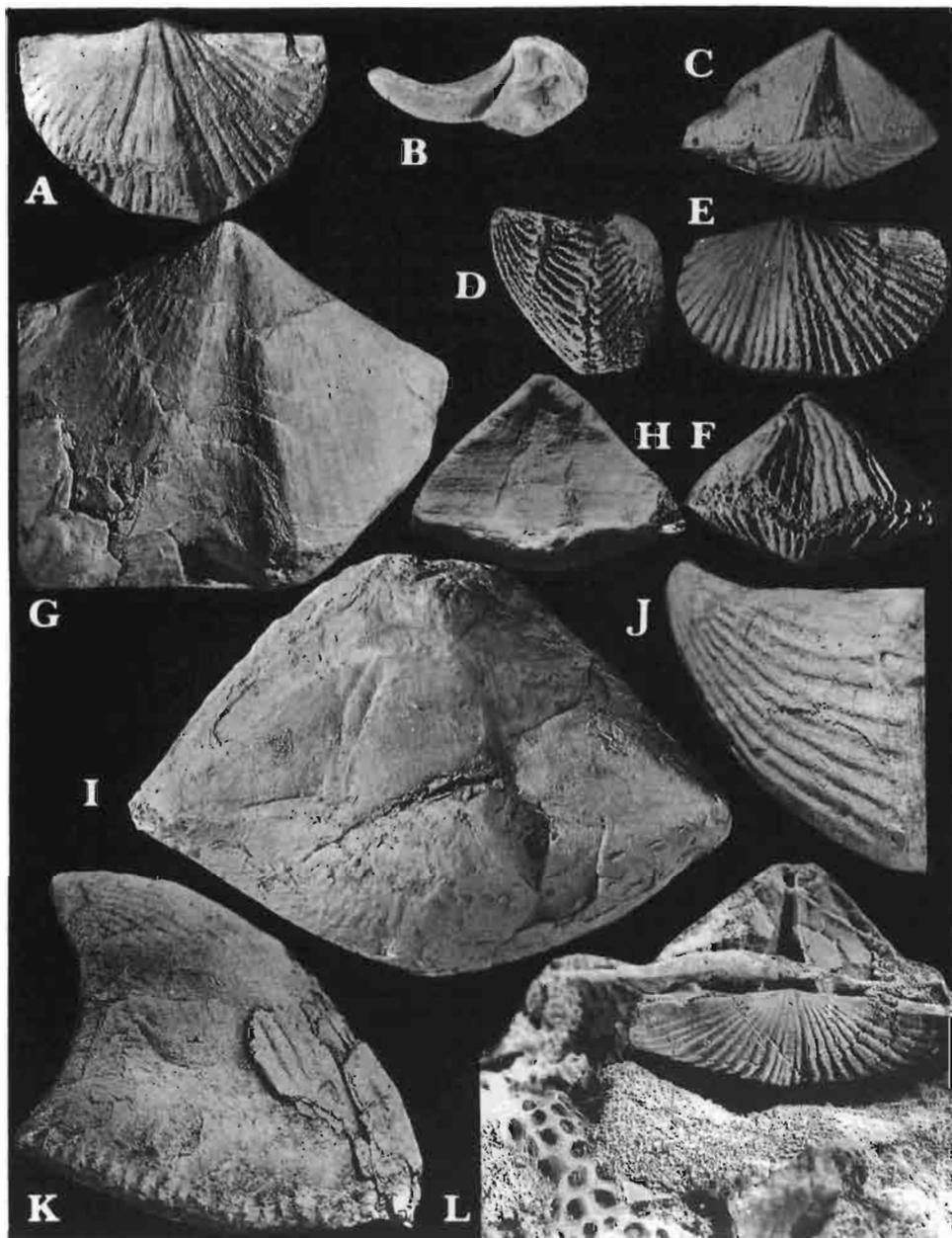
Both valves are covered with more or less regular concentric rugae (3-4 per 5 mm), and alternately and densely arranged (3-5 per 5 mm of the concentric belt) and subdued spine ridges. Occasionally, a ventral median ridge with enlarged spines is developed. Growth lines are fine (4-8 per 1 mm). Elongated sockets and more inconspicuous spine ridges ornament the exterior of the dorsal valve.

The bilobate cardinal process is low, with gently diverging lobes, the alveolus and inner socket ridges being weak. The distinctly developed brevisseptum represents the posterior 0.6 to 0.8 of the length of the shell. The adductor muscle field with two obliquely elongated scars is rarely perceptible. The remaining surface bears small endospines, in peripheral parts joined with one or two marginal corrugations. The interior of the ventral valve reveals deep, elongated and subparallel adductor scars.

Variability.— Deviations from the regular quincuncial plan of the spine bases are its most significant expression, sometimes being combined with a varying appearance of rugae and spine ridges, and with incipient median ridge. Specimens from Marzysz are markedly small-sized (width below 20 mm) and show more irregularly distributed spines (Fig. 1E-F).

Remarks.— The new species is closely similar to the type species of the genus, *P. oreliana* (Miller 1871) from the Russian Famennian (Nalivkin 1947; Sokolskaja 1948; Lyashenko 1959; Muir-Wood & Cooper 1960). Thicker concentric rugae and a tendency to develop spine ridges suggest

Fig. 17. □A, C-F, L. *Tenticospirifer utahensis* (Meek 1876, dorsal, anterior, posterior and lateral views, GIUS 4-229/O-1 (A), GIUS 4-230/O-11 (C-F), GIUS 4-239/O-2 (L); Givetian Chęciny Beds (A, C-F) and Frasnian upper Sitkówka Beds (L), Sosnówka (set B; A), Zegzelogóra (set



A: C-F), and Sitkówka-Kostrzewa (set C: L). □B. *Crurispirina 'inflata'* (Schnur 1853) morphotype A, ventral interior, GIUS 4-211/23; Givetian Jaźwica Mbr., Jaźwica (set B). □G, I-K. *Cyrtospirifer* ex gr. *aperturatus* (Schlotheim 1820), fragmentary shells in anterior, posterior and lateral views, GIUS 4-231/1 (G), 2 (I), 3 (K); Chęciny Beds, Stokówka (set C). □H, J. *Tenticospirifer lagoviensis* (Gürich 1896), small specimen in posterior view (H), and coarse-ribbed ventral valve in lateral view (J), GIUS 4-218/11 (H), 21 (J); Givetian *Tenticospirifer* Limestone Level, Łągów. All × 2.

an affinity to the poorly-known, monospecific genus *Strophoproductus* Nalivkin *sensu* Muir-Wood & Cooper (1960). A strongly projecting beak, lack of double-rowed spine arrangement in posterior-lateral parts and large sizes of shell are also suggestive of a transitional position of the Polish forms.

P.(?) sobolevi sp. n. is probably closest to the Frasnian Uralian productellids assigned by Nalivkin (1947, 1951) to *Waagenoconcha murchisoniana* (*non* Koninck 1838; see Brousmiche 1973). The Polish species exhibits distinctly smaller ventral umbo and more regular spine pattern. *Praewaagenoconcha speciosa* (Hall 1864) displays a reduced ventral beak and finer ornamentation, exaggerated by smaller size of shells (see Hall & Clarke 1892; Martynova 1961; Baliński 1979).

Distribution.— See p. 300.

Family Atrypidae Gill 1871

Genus *Desquamatia* Alekseeva 1960

Desquamatia globosa (Gürich 1896)

Revised diagnosis.— Shell of medium size (for the genus), typically subcircular to slightly transversely elongated, with variable convexity relationships from equibiconvex to strongly dorsibiconvex. Ribs fine ($z/20$ mostly 12-18), not very high and generally uniformly wide, bifurcating in the ventral valve, and mainly intercalating in the brachial valve. Growth lamellae inserted regularly at intervals 2-4 mm, not very sharply deflected from the shell surface, more or less frilled. Dental plates long, low, lateral cavities small. Pedicle collar is lacking.

Remarks.— A succession of two new subspecies *D. g. aequiconvexa* and *D. g. sitkowskensis* is recognized in the geographically separated Sitkówka basin. Such interpretation seems to be more biologically realistic than possible inclusion of the Sitkówka atrypids into similar species known from Australia, USA or Western Europe. In effect, the range of the species is significantly widened (Figs 6-7) in comparison to that proposed by Baliński (*in* Racki & Baliński 1981).

Desquamatia globosa globosa (Gürich 1896)

Figs 5C, E, J-K, 6-7.

Atrypa reticularis Linne var. *globosa*: Gürich 1896: p. 270 (partim).

Desquamatia (Seratrypa) globosa (Gürich); Baliński (*in* Racki & Baliński): pp. 197-201.

Text-figs 16-20, Pls 8: 1-4, 9: 2-3, 5-7, 9-10.

Desquamatia (Seratrypa) aff. globosa (Gürich); Baliński (*in* Racki & Baliński): pp. 201, Pl. 9: 4.

Material.— About 80 whole and 160 almost complete shells, above 500 fragments.

Emended diagnosis.— Large (W up to 45 mm), 'Seratrypa'-type, strongly dorsibiconvex (TI = 0.65-0.75; EI = 0.6), infrequently globose, with anaclinal interarea, appressed beak, and significantly uniplicate anterior commissure.

Variability.— Despite a wide range of variability (Racki & Baliński 1981: p. 193) only two gross varieties are distinguished here within the subspecies

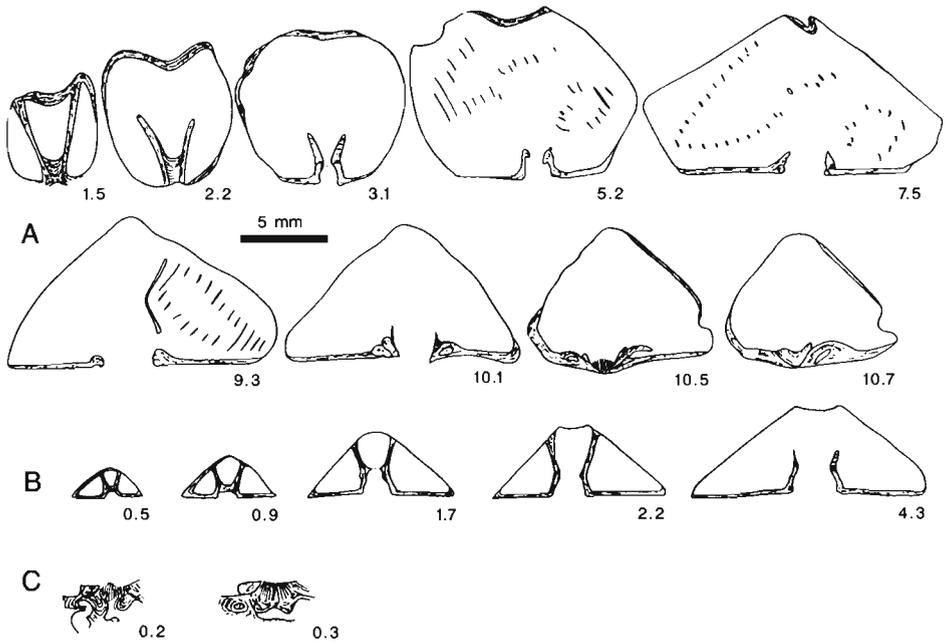


Fig. 18. *Tenticospirifer lagoviensis* (Gürich 1896), parallel (A-B) serial sections, and enlarged cross sections of dorsal valve (C) to show cardinal process, GIUS 4-218/12 (A), 13 (B), 14 (C); Givetian *Tenticospirifer* Limestone Level, Łągów.

as being potentially important from the stratigraphic standpoint: (A) older, with more elongated shell from the Zegzelogóra-Sosnówka area, and (B) generally wider shell variant dominating in the Chęciny and Sitkówka (atrypid bed B-I) sections.

Remarks.— The subspecies occurs in the Chęciny Beds (see Baliński *in* Racki & Baliński 1981). In the highest part of the type site (Góra Zamkowa, set J) a few large-sized specimens are found similar to the atrypid-rich set F. A diminutive form identified as *D. (S.)* aff. *globosa* by Baliński from the set J is included in this subspecies being stratigraphically variably in the shell size.

Distribution.— See p. 302.

Desquamatia globosa aequiconvexa subsp. n.

Figs 6B, 7, 8A-F.

Holotype: GIUS 4-238a/D-1; Fig. 8B-D.

Type horizon and locality: Chęciny Beds, Kowala Formation, latest Givetian; Sitkówka, old Kostrzewa quarry, set B₁ (atrypid shell bed B-II; Atrypid-Crinoid Limestone Level), Poland.

Derivation of name: From Latin *aequa* and *convexus* to underline the equal convexity of both valves.

Material.— Six complete and 13 almost complete shells, approximately 30 fragments.

Diagnosis.— Mostly equibiconvex (TI = 0.5-0.7; EI=0.5) medium-sized shells with a tendency to develop posterolateral ears at cardinal ex-

termities, interarea anaclinal, weakly curved ventral beak and possibly exhibiting only short frills. Some specimens are markedly gently inflated and/or coarsely ribbed.

Remarks.— The subspecies is restricted to the bed B-II in Sitkówka, where were found also specimens morphologically transitional to the nominative form: globose, but almost equibiconvex, with curved beak and weak ventral sulcus. Weakly-convex morphotypes intermediate between the subspecies *D. g. globosa* and *D. g. aequiconvexa* occur in the shell beds F-III at Chęciny (Racki & Baliński 1981: Pl. 8: 3) and B-III of Sitkówka. However, the Sitkówka form is markedly distinct in having less inflated, evenly biconvex shells with variably curved, sometimes almost suberect beak.

The considered 'Synatrypa-type' form is most similar to *Desquamatia (Synatrypa) kimberleyensis* (Coleman 1951) from the Frasnian of Australia (Coleman 1951; Roberts 1971; Grey 1978). The Holy Cross Mountains atrypids are larger-sized, more coarsely-ornamented, especially in growth lamellae, and exhibit more delicate internal cardinal characters.

Distribution.— See p. 302.

Desquamatia globosa sitkowkensis subsp. n.

Figs 6-7, 9, 14J.

Atrypa desquamata var. *sonata* (sic!) Schnur; Sobolev 1909: p. 487.

Holotype: GIUS 4-238b/D-8; Fig. 9A-B.

Type horizon and locality: Chęciny Beds, Kowala Formation, latest Givetian to earliest Frasnian transition; Sitkówka, old Kostrzewa quarry, set B₂ (shell bed B-III; Atrypid-Crioid Level), Poland.

Derivation of name: From the village Sitkówka, the type locality.

Material.— Fifty five complete and 110 almost complete shells, 20 valves, ca. 100 fragments; all silicified.

Diagnosis.— The medium-sized variety of *D. globosa* displays a subcircular to elongate outline, dorsibiconvex shell (TI = 0.55-0.6, EI=0.6) with suberect beak and low, well visible interarea. Variably ornamented with fairly thick costae ($z/20=11-12$). Very distinct, widely distributed (3-5 mm) and infrequently deflected frills-like growth lamellae, up to 25 mm.

Variability.— The material documents very broad variations in the shell shape and ribbing, typical of many atrypids. There are singular specimens morphologically transitional to both the remaining subspecies of *D. globosa*, but the main diagnostic features of *D. g. sitkowkensis* comprise a more distinct ribbing and frill-like widely spaced growth lamellae, and a protruding beak.

Remarks.— The elongate-oval shaped specimens from Sitkówka show some similarity to *Desquamatia (Seratrypa) pectinata* Copper 1967 from the Givetian to Frasnian transition of the Bergisches Land (Copper 1967b) and Ardennes (Godefroid & Jacobs 1986). The Variscan species is distinguished by an elongated shell with incurved beak, finer ribbing ($z/20 = 12-16$), and shorter dental plates and socket ridges.

Some finely ribbed, sub-semicircular shells showing deflected lamellae of ragged appearance suggest relations with the *Desquamatia (Independatrypa) zonata* group from the Eifel, as apparently noticed by Sobolev (1909). The latter subgenus includes species with large-sized, subquadrate and finely-costate shells (see Copper 1966b, 1973, 1978; Norris & Uyeno 1983; Godefroid & Jacobs 1986). Givetian atrypids from Kuznetsk Basin assigned to *D.(I.) magna* (Tien 1938) by Alekseeva (1962) reveal conspicuous widely spaced growth lamellae, like *D. cf. magna* from Jażwica (Fig. 5D).

Distribution.— See p. 306.

Family Cyrtospiriferidae Termier & Termier 1949

Genus *Tenticospirifer* Tien 1938

Tenticospirifer lagoviensis (Gürich 1896)

Figs 17H-J, 18, 19D-K.

Spirifer canaliferus var. *lagoviensis*; Gürich 1896: p. 249, Pl. 9: 4.

Spirifer tentaculum var. *lagoviensis* Gürich; Gürich 1901: p. 380.

Spirifer aperturatus Schlotheim; Samsonowicz 1917: p. 11.

Cyrtospirifer canaliferus var. *lagoviensis* Gürich; Vandercammen 1959: p. 97.

Spirifer mediotextus d'Archiac & Verneuil; Kortański 1959: pp.272, 274.

Proposed neotype: GIUS 4-218/1; Fig. 19D-G.

Type horizon and locality: Late Givetian, *Tenticospirifer* Limestone Level (equivalent of the Jażwica Member); Łagów, eastern escarpment of the Łagowica river, Poland.

Material.— Seven almost complete shells, 10 dorsal valves, 50 fragments; mostly deformed.

Diagnosis.— Medium-sized tenticospirifers characterized by a transversely elongated shell with varied, but typically thick costae and rather shallow tongue; fold and sulcus distinctly differentiated.

Description.— Medium-sized (up to 20 mm long), semipyramidal, transversely-trapezoidal shells display flat, close to catacline ventral interarea and gently incurved beak. The sulcus and fold are moderately developed but sharply bounded, the tongue is lowly arched. The ornamentation consists of coarse, simple, broadly-rounded costae on the flanks (9-11 in number) and wider ones, subdued, and bifurcating in the sulcus and fold (6-10 in number).

The delthyrial plate is concave, small; the dental plates are thin, diverging, extending not beyond the mid-length of the valve. The cardinal process of moderate height, deeply striated, hinge plates are rectangular, adherent to the basis of the cardinal process. Crura long, bent, spiralium consists maximum of 12 coils.

Variability.— *T. lagoviensis* is typified by a varied shell shape (TI – 0.91-1.36; WI – 1.6-2.1), thickness of costae (z/ap – 7-13, n_s – 5-12; for shells being 10-15 mm long) and distinctness of sulcus and fold.

Remarks.— Gürich (1896) based his description of *T. lagoviensis* on immature specimens (length 12.5 mm for the figured one) which resulted in incomplete characteristics, particularly in respect to the radial ornament.

The Gürich's species may be rather easily separated from other congeners. *T. tentaculum* (Verneuil 1845), type species of the genus from the Middle Frasnian of Russia (Nalivkin 1941, 1947; Pitrat 1965) and from the Frasnian of Ardennes (Vandercammen 1959) is distinguished by fine costation ($z/ap - 12-16$) and a slightly less transverse shell (for illustrated individuals W.I. is ca. 1.4-1.7). The coarse ornamentation combined with small shell sizes differs the Holy Cross Mountains form from the Russian species *T. markovskii* Nalivkin 1947 (Rzhonsnitskaja 1952; Lyashenko 1959); significantly shallower sulcus differs it from others, e.g. *T. lictor* Nalivkin 1930 and *T. tribulatus* Lyashenko 1959, as also from *T. columnaris* Roberts 1971 from the Frasnian of Australia.

Distribution.— See p. 314.

Family Ambocoeliidae George 1931

Classification of these small smooth spiriferids has been a subject to controversies because of difficulties in evaluating particular characters (e.g. Vandercammen 1956; Havliček 1959; Veevers 1959b; Pitrat 1965; Dürkoop 1970; Johnson & Trojan 1982) and ambiguities regarding indications of several type species (Jux & Strauch 1965; Bublitchenko 1974). Some questions, especially concerning internal morphology were recently resolved by Glodman & Mitchell (1990), but there is still a need for substantial taxonomic revision.

This is exemplified by the crucial for systematical study problem of micro-ornamentation. Its character depends not only on simple exfoliation (e.g. Gürich 1896; Biernat 1953; Vandercammen 1956) but even surficial shell weathering (Baliński 1975). Papillae appear to develop in effect of gradual destruction of originally smooth or striated external shell layer (Brunton 1976). A removal of the primary layer may produce a secondary radial ornament. Thus the nature of spinose and striated sculpture requires always explanation in diagnoses of genera (e.g. of *Ilmenispina*; see Baliński 1975; Ficner & Havliček 1978).

It appears that within the subfamily Rhynchospiriferinae *sensu* Glodman & Mitchell (1990) at least two distinctive groups can be distinguished with contrasting types of original micro-ornamentation: (1) delicately radially striated (*Rhynchospirifer*, *Kosirium*, *Moravilla*, ?*Ilmenia*, ?*Ladija*, ?*Choperella*); and (2) microspines and papillae in concentric or more or less radial-alternative (quincunxial) patterns (*Emanuella*, *Crurispina*, ?*Ambothyris*). The first generic suite only seems to be marked by dental plates (and partly cruralium), and correspond to original concept of the subfamily given by Paulus (1957; see also Fickner & Havliček 1978; Johnson & Trojan 1982).

Genus *Ilmenia* Nalivkin 1941

Ilmenia(?) *elatior* (Gürich 1896)

Figs 20A-C, E-H, 21A, 22, 23A-C, G-I, 24C-D, F-G.

Martinia inflata Schnur var. *elatior*; Gürich 1896: p. 265 (?partim), Pl. 9: 8.

Spirifer aff. *hians* (von Buch); Sobolev 1909: p. 470 (?partim).

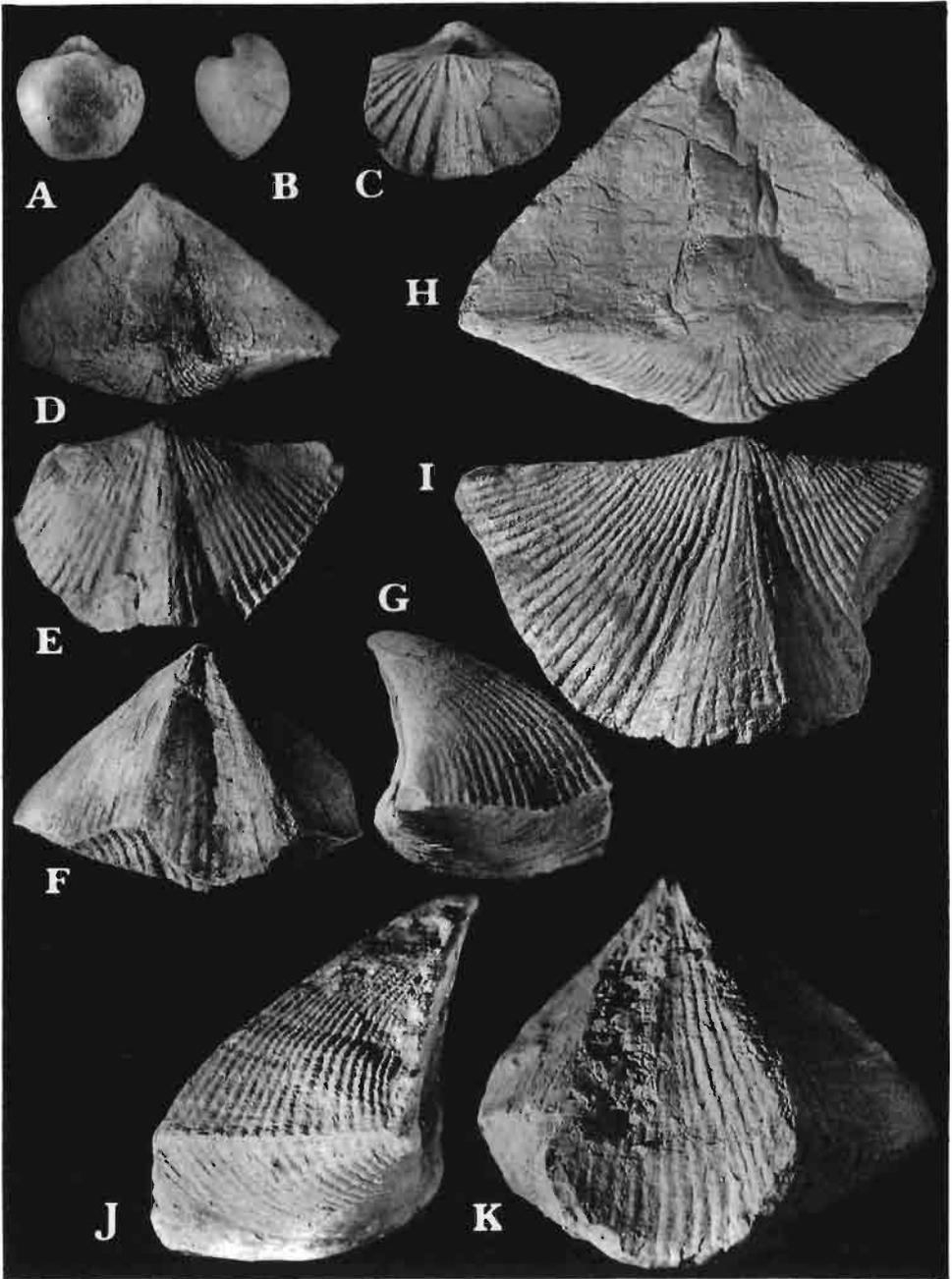


Fig. 19. □A-B. *Crurispingina 'inflata'* (Schnur 1853) morphotype A, dorsal and lateral views, GIUS 4-211/1; Givetian Jazwica Mbr., Jazwica (set B). □C. Coarsely-plicated spiriferid (?*Mucrospiriferidae*) in dorsal view, GIUS 4-239/O-4; Frasnian upper Sitkówka Beds, Sitkówka-Kostrzewa (set C). □D-K. *Tenticospirifer lagoviensis* (Gürich 1896), anterior, dorsal, lateral and posterior views: D-G - neotype GIUS 4-218/1 (L=1.2 mm, W=ca. 29 mm, T=24.8 mm, $Z_{ap}=10$, ns=?16); GIUS 4-218/2 (H-K); Givetian *Tenticospirifer* Limestone Level, Łagów. All $\times 2$.

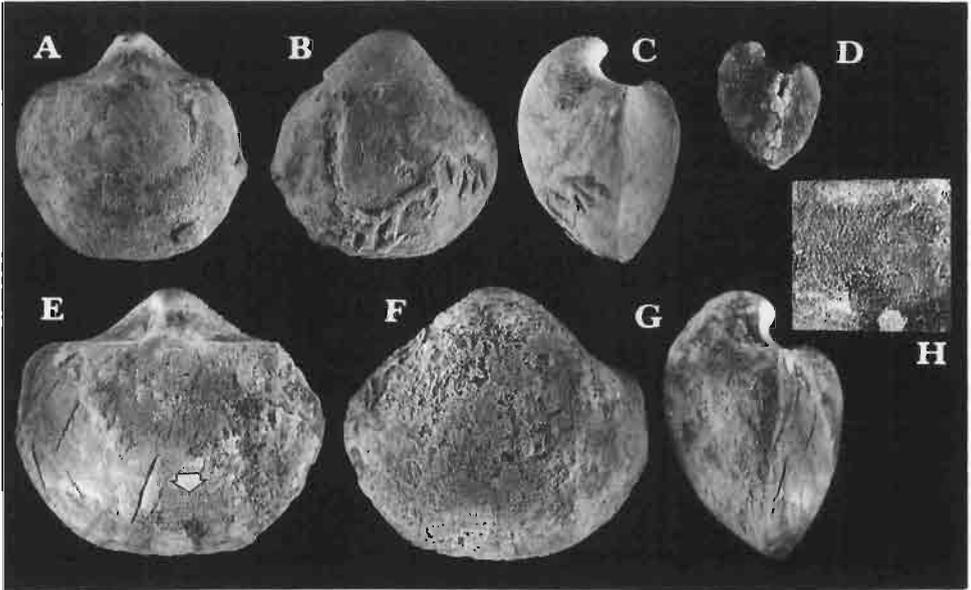


Fig. 20. □A-C, E-H. *Ilmenia(?) elatior* (Gürich 1896), dorsal, ventral and lateral views (A-C, E-G), with visible epizoic bryozoans (B-C), and magnified shell fragment (H) to show secondary microornament (E). GIUS 4-193/1 (A-C), 2 (E-H); Givetian Ambocoeliid Limestone Level, Góra Zamkowa (set A₁). □D. *Crurispina 'inflata'* (Schnur 1853) morphotype A, juvenile specimens in lateral view, GIU 4-176b/21; Givetian Dziejwki Limestone, Siewierz (set D). All × 3 except for H that is × 6.

Proposed neotype: GIUS 4-193/15; Fig. 23A-C.

Type horizon and locality: Middle Givetian (late part), topmost *Stringocephalus* Beds (Ambocoeliid Limestone Level), Kowala Formation; Chęciny, Góra Zamkowa (western quarry, set A₁), Poland.

Diagnosis.— Fairly large (up to 20 mm long), subcircular to transversely oval shells with well developed dental lamellae and distinctive secondary radial striation.

Material.— Thirty six complete and 70 incomplete shells, some asymmetrical (Fig. 24C-D), above 100 fragments.

Description.— Rather large-sized (length less than 20 mm), ventribiconvex shells are rounded to slightly transverse (WI – 0.95-1.1). The subdued median furrow on the ventral valve weakly curves the anterior commissure; dorsal fold is almost not discernible; area is apsacline, delthyrium bordered by deltidial plates, with an apical plug.

The shell surface is originally smooth, but due to a progressive weathering radially arranged lenticular microspines (papillae) appear passing to radiating striae (3-4 per 1 mm; Fig. 20H) and/or closely spaced tubercles (Fig. 24F; also Gürich 1896: Pl. 9: 8b).

Dental plates are overall well developed, with rare gradations into tooth ridges. The cardinal process is like a small triangular weakly striated knob, dental sockets are of intermediate-type (cf. Goldman & Mitchell 1990).

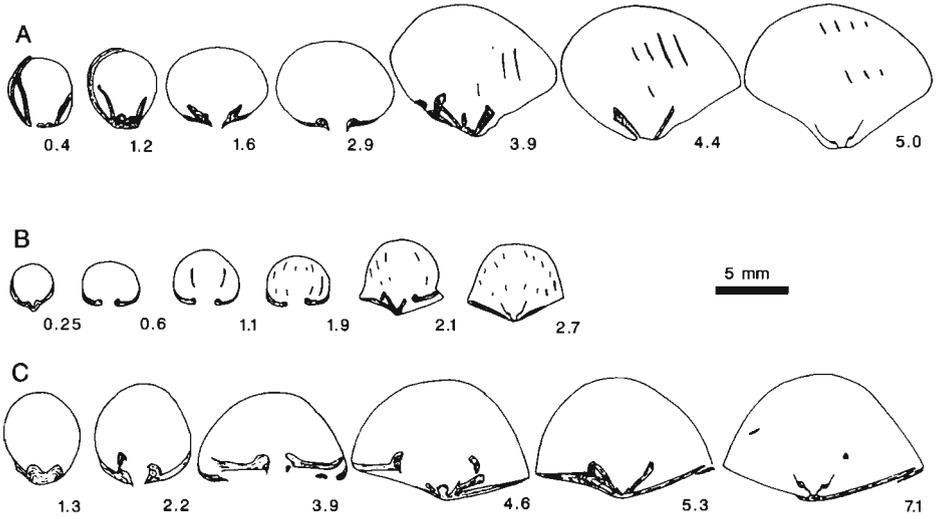


Fig. 21. Serial sections of ambocoeliid spiriferids. □A. *Ilmenia(?) elator*, GIUS 4-193/24; Givetian Ambocoeliid Limestone Level, Góra Zamkowa (set A). B-C. □*Crurispina 'inflata'*, GIUS 4-211/31 (morphotype A; B), GIUS 4-220/C-11 (morphotype B; C); Givetian Jażwica Mbr., Jażwica (set B; B), and lower Sitkówka Beds, Poślówice (set C; C).

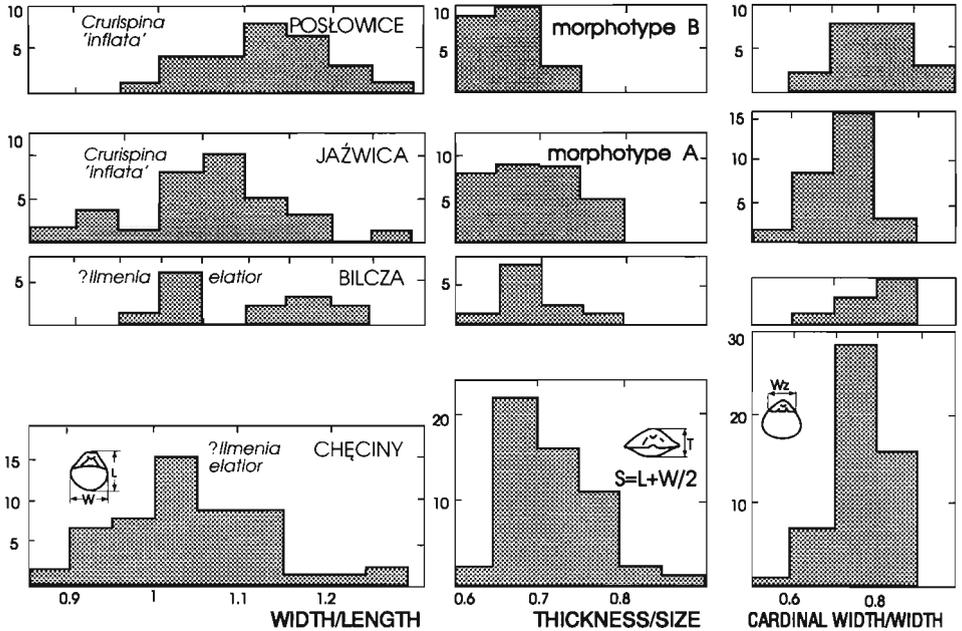


Fig. 22. Frequency distribution of principal shell indices for ambocoeliid species from different sites in the Holy Cross Mts.

crural plates typically disjunct, subparallel to slightly divergent, each spire has 4-5 coils.

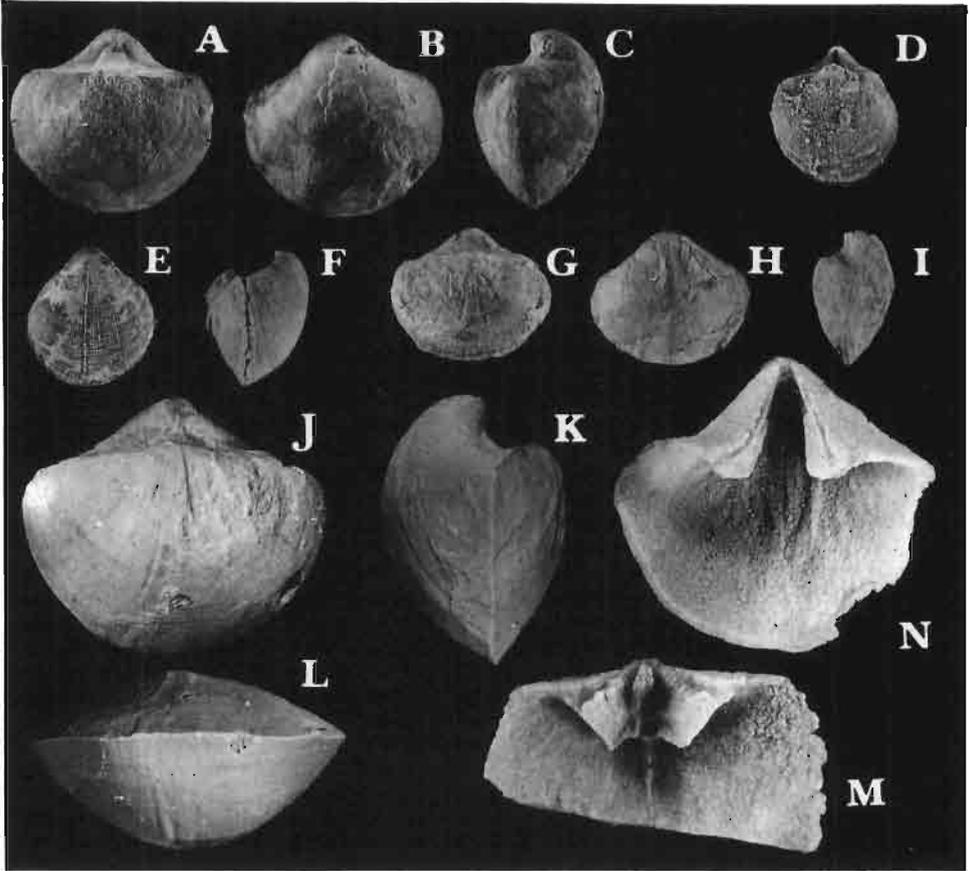


Fig. 23. □A-C, G-I. *Ilmenia(?) elatior* (Gürich 1896), dorsal, ventral and lateral views; A-C – neotype GIUS 4-193/15 (L=13.6 mm, W=13.8 mm, T=10.2 mm, H=2 mm); GIUS 4-184/1 (G-I); Givetian Ambocoeliid Limestone Level, Góra Zamkowa (set A₁; A-C) and Bilcza-II (set A; G-I). □D-F, M-N. *Rhynchospirifer hians* (von Buch 1834), dorsal, ventral and lateral shell views, and ventral and dorsal interiors. GIUS 4-176a/1 (D-F), 19 (M), 20 (N); Givetian Dziewki Limestone, Siewierz (set D). □J-L. *Crurispina 'inflata'* (Schnur 1853) morphotype B, dorsal, lateral and anterior views, GIUS 4-217/A-1; Givetian lower Sitkówka Beds, Poślowice (set C). All × 2 except for M-N that are × 5.

Variability.– The outline of the shell and the length of the hinge line and to lesser degree also size of dental plates belong to the most variable features (Fig. 22).

Remarks.– Gürich (1896) and Sobolev (1909) have not described details of the interior for specimens from Chęciny, but the size of the specimen illustrated by Gürich, as well as descriptions of its sculpture allow us to identify the variety 'elatior' with the older ambocoeliid from Góra Zamkowa. In all probability, the above authors collected both ambocoeliid species from Chęciny (see Sobolev 1909: Pl. 5: 8), and some other ambocoeliids from Siewierz and Kostomłoty were included in the Gürich's variety.

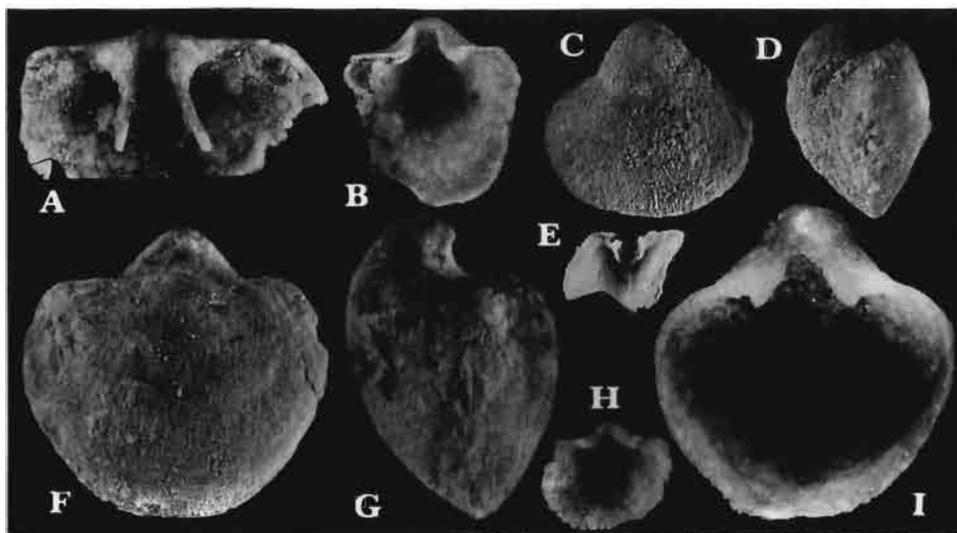


Fig. 24. □A-B, H-I. *Crurispinga 'inflata'* (Schnur 1853) morphotype A, interiors of dorsal (A) and ventral (B, H-I) valves, GIUS 4-176b/19 (A), 20 (B), 22 (H), 23 (I); Givetian Dziewki Limestone, Siewierz (set D). □C-D, F-G. *Ilmenia(?) elatior* (Gürich 1896), ventral, lateral and dorsal views, note shell asymmetry (C), GIUS 4-193/7 (C-D), 8 (F-G); Givetian Ambocoeliid Limestone Level, Góra Zamkowa (set A₁). □E. *Rhynchospirifer hians* (von Buch 1834), dorsal interior of deformed valve, GIUS 4-176a/18, Givetian Dziewki Limestone, Siewierz (set D). All × 3 except for E that is × 1.3.

The species under discussion is ultimately assigned to the genus *Ilmenia*, following interpretations of the genus by Dürkoop (1970), Ficner & Havlíček (1978: p. 80), and Johnson & Trojan (1982: pp. 128-129). Its probable affinities with the genus *Ladija* remain disputable. *I.(?) elatior* seems to be close to the 'right-Rhenish' morphotype of *Spirifer inflatus* Schnur 1853 *sensu* Leidhold (1928; see also Paeckelmann 1913) and to *Spirifer decipiens* Torley 1934. Any comparison with the Rhenish ambocoeliids (also including *Martinia inflata* (Schnur 1853) of Jux & Strauch 1965; ?*Emanuella*; U. Jux, letter communication 1984) is hampered by an unclear nature of their sculpture. Other similar ambocoeliids exhibit primarily concentric ornament (e.g. *Thomasaria gibbosa* Vandercammen 1956) and/or more incurved ventral beak (*Ilmenia perlaevis* Nalivkin 1930; Lyashenko 1959).

Distribution.— See p. 314.

Paleoecology

Extensive lateral variation of biofacies contrasted with the dominance of low energy lithofacies (Racki 1993) clearly points to more subtle ecologic control of the distribution of fossils in the Kowala Formation. The brachiopod occurrences examined are close in taphonomic terms to the shell-rich

beds and Kadzielnia bioherms described by Racki & Baliński (1981), Szulczewski & Racki (1981) and Racki (1985, 1986a). They typically represent relicts of brachiopod biostromes (*sensu* Aigner *et al.* 1978) slightly modified due to a current reworking and frequently bioturbated. Such preservation is widespread among extant brachiopod communities (Noble & Logan 1981).

The recognition of original biotic relationships is facilitated by the monospecific or high-dominated nature of most of the brachiopod occurrences, correlated with a facies-type. These are frequently repeated in sequentially, recurrent communities. The brachiopod units are grouped into two intergrading types (cf. Kauffman & Scott 1976):

- (1) bottom-level assemblages (Racki & Baliński 1981), where brachiopods have formed the main macrofaunal element of the original benthos;
- (2) reef-related associations (Racki 1985), where brachiopods were subordinate, but still represent a significant component of the organic buildup community (for the principal Assemblages see Racki 1993: Figs 12, 16, 22). The main exception is the productellid association being a part of the echinoderm-dominated open shelf biota.

Lagoonal habitats

Brachiopod ecology in restricted-shelf facies has been discussed previously (Racki 1986a); only new data and a regional account are presented herein.

Stringocephalus 'burtini' Assemblage (Fig. 27).— Typical sites: Jurkowiec-Budy (set E) and Brudzowice-Dziewki (sets C-D). The giant Devonian terebratulids are known chiefly from high-density accumulations of single valves, mainly in concave-up configurations related to biostromal levels (e.g. Sowie Górki, set B). Rare stromatoporoids, largely *Amphipora*, and shelly fossils, as well as abundant ostracods, including leperditiids, belong to the most frequent associated fossils. Articulated shells in assumed growth, beak-down positions are far less common, restricted mostly to macrofossil-poor micrite facies (Sowie Górki, set A).

Ilmenia(?) elatior Assemblage.— Typical site: Bilcza-3 hill (set A). The ambocoeliids occur in thin lumachelle intercalations composed of more or less reworked shell material. The assemblage, widespread in the Ambocoeliid Level in the SW-part of Holy Cross Mountains, includes also stromatoporoids, gastropods and ostracods. The presence of epizoic bryozoans, microcornids (Fig. 20B-C), and fine (?) algal borings in approximately one fifth of collected specimens is notable for some sites (Góra Zamkowa, Góra Sołtysia). They are distributed mostly along the anterior commissure of dorsal valves which suggests an encrustation in reclining, normal (i.e. ventral valve down) life positions (Ivanova 1962; Caldwell 1967; McGhee 1976). Broad intraspecific variability and sporadic asym-

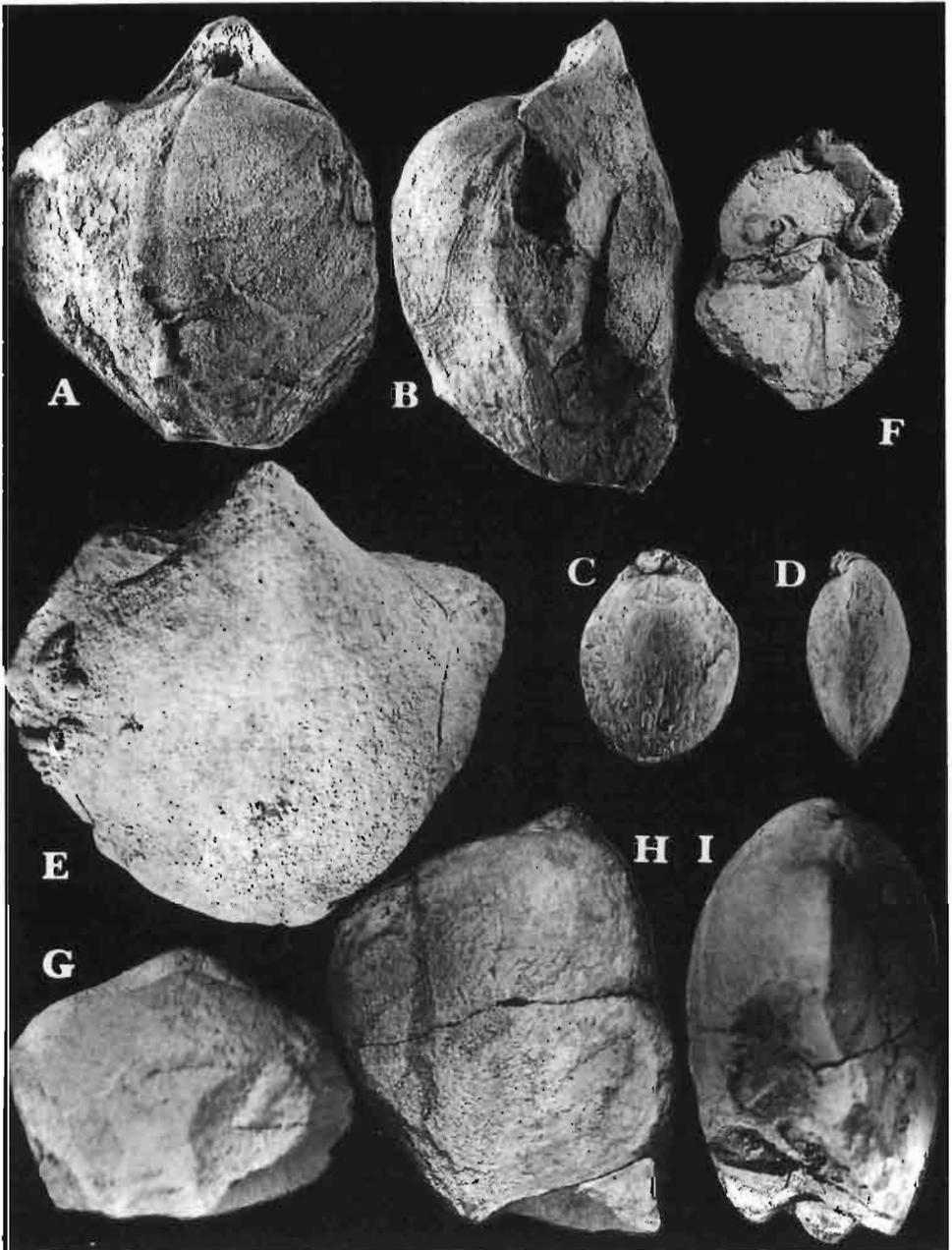


Fig. 25. ▴A-B. *Parastringocephalus* cf. *parasulcatus beyrichi* Struve 1982, dorsal and lateral views, GIUS 4-175/S-1; Givetian Dziejwki Limestone, Siewierz (set C). ▣C-D. '*Rensselandia*' sp., dorsal and lateral views, GIUS 4-175/O-1; Givetian Dziejwki Limestone, Siewierz (set C). ▢E. *Stringocephalus* sp., ventral view of small shell, GIUS 4-163/S-1; Givetian *Stringocephalus* Beds, Jurkowice-Budy (set E). ▣F-I. *Rensselandia* cf. *circularis* (Holzapfel 1908), interior of umbonal portion (F; note discrete cardinal plates), and fragmentary shells in dorsal and lateral views, GIUS 4-162/10 (F), 2 (G), 1 (H-I); Givetian *Stringocephalus* Beds, Jurkowice-Budy (set A). All $\times 2$ except for A-B which is in natural size.

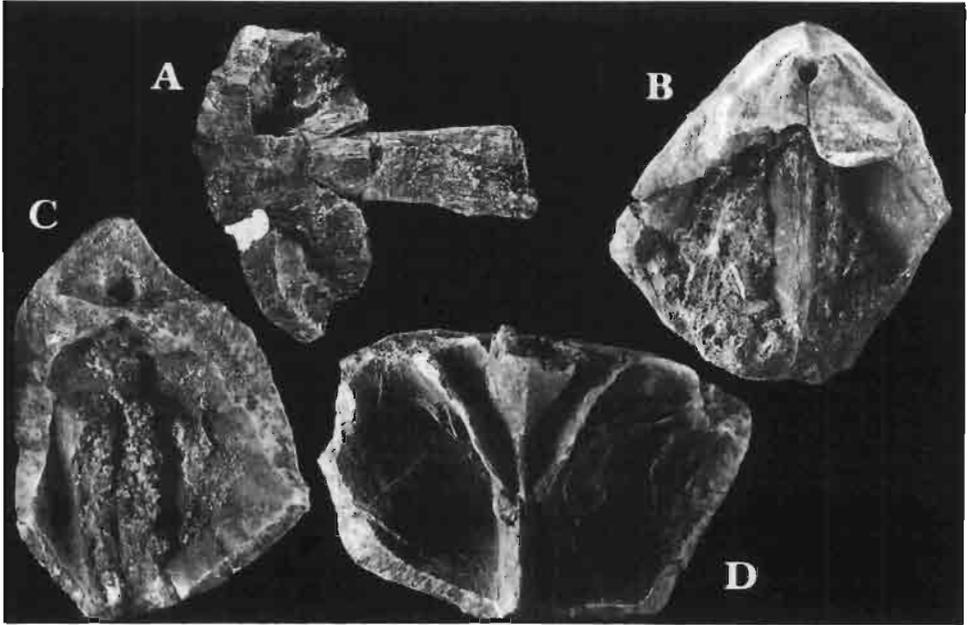


Fig. 26. *Stringocephalus* sp., anterior view of dorsal valve (A), interior of ventral valves (B-C), fragmentary dorsal interior (D); Givetian *Stringocephalus* Beds, Czarnów (set A); taken from Filonowicz (1973: Pl. 26: 254-255). All natural size.

metrical individuals evidence very high population density (Biernat 1953, 1971; McCommon 1970).

***Metabolipa* assemblage.**— Typical locality: natural outcrops in the Pokrzywianka river valley near Wojnowice-Podgórze (Racki 1986a: Fig. 4). This monospecific fauna is limited to the eastern part of the region. It occurs in varied 'cryptalgal' limestones only with amphiporids, including the laminite-oncolite level (Racki & Soboń-Podgórska 1993: Fig. 2C-E). High disarticulation seems to be a result of the weakness of the hinge apparatus rather than of high energy events. Great juvenile mortality may reflect inhospitable life conditions of high stress in extremely shallow-water and restricted habitats atypical of the gypidulids (Racki *et al.* in press a).

***Rensselandia* assemblage.**— Type site: Jurkowice-Budy Quarry (set A). This is the only lagoonal assemblage with some open-marine faunal indicators, chiefly diminutive crinoid remains, and reworked shell material (terebratulids, ?possibly ambocoeliids; Racki 1986a: Pl. 1: 1). Rensselandiids occur almost exclusively in the lagoonal-reef facies of southern Poland. Hence, the fauna can still be considered as a restricted-marine assemblage on the basis of inferred by Fürsich & Hurst (1980) euryhalinity of the large Devonian terebratulids. Probably, the brachiopod banks thrived behind crinoid meadows, in a groove at the marginal shoal that

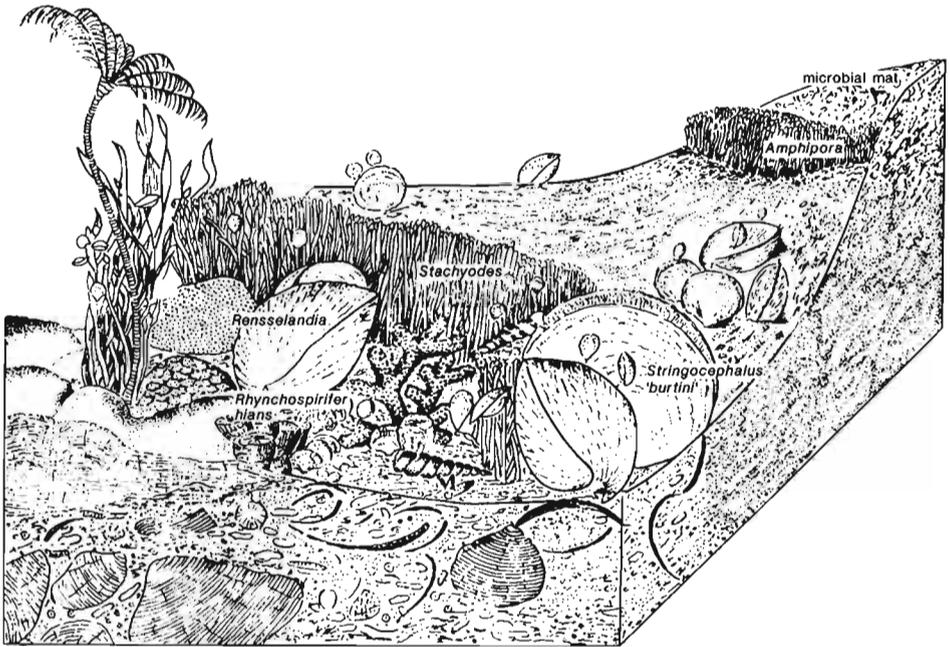


Fig. 27. Idealized biotope reconstruction of the Middle Givetian *Stringocephalus 'burtini'* Assemblage and *Rhynchospirifer hians* association within the *Stringocephalus* biostromal bank.

rimmed the shelf lagoon (see also data from the Siewierz area in Racki *et al.* in press b).

Stromatoporoid buildup habitats

Brachiopods are rarely numerous in the stromatoporoid limestones, and they populated only isolated mud patches within organic framework (Racki 1985).

***Rhynchospirifer hians* association** of the *Hermatostroma-Caliapora*-*Pseudohexagonaria* Assemblage (Fig. 27).— Typical site: Jurkowiec-Budy (set E). Probably the nominal species was linked mostly with dendroid stromatoporoid biostromes, like that at the Siewierz locality (set D). In Jurkowiec-Budy it is accompanied by various fossils comprising corals, gastropods, trilobites, ostracodes, calcisponges, crinoids and tentaculites, and so on (Baliński 1973; Racki 1993). The shells are frequently bored by algae(?), sometimes incrustated by auloporids, and/or bear micrite coatings.

The index species is strongly predominant (about 95%, Baliński 1973; see Fig. 32) among all brachiopods in Jurkowiec-Budy being associated with rare but large stringocephalids and very scarce other ambocoeliid, athyrid and rensselandiid species. In the Dziewki Limestone only infre-

quent stringocephalids co-occur so the influence of a lagoonal regime is apparent.

The association comprises brachiopods of two ecomorphologic types: (1) small, striated or smooth, possibly mostly attached ambocoeliids, and athyrids, and (2) large-sized, smooth and free-lying terebratulids in normal or reversed positions (ventral valve down; Baliński 1973). The biostrome-dwelling ambocoeliids might possess a short pedicle enabling strong attachment to the hard organic substrate (cf. Caldwell 1967) that probably contrasts with level-bottom representatives of the eurytopic family studies of living brachiopods point to a variable form and function of pedicle (Richardson 1981), frequently difficult to deduce from the skeletal morphology.

As pointed out by Baliński (1973), the size of adult ambocoeliids not more than 13 mm and their high juvenile mortality combined with extensive variability are suggestive of high-stress life conditions. This might be due to oscillatory environmental changes, primarily in salinity. *R. hians* association was a typical member of more or less diversified biota building stromatoporoid shoals in a low energy conditions as stated by Kaźmierczak (1971). As to the other biostrome dwellers, the high frequency of vagile herbivores and scavengers (with *Murchisonia coronata* among gastropods) is remarkable.

Crurispina 'inflata' association of *Stachyodes* Assemblage.— Typical site: Jaźwica quarry (set A). This diminutive eurytopic ambocoeliid (morphotype A) occurs as scattered valves or their accumulations in some *Amphipora* beds (Góra Zamkowa, set A₁; Siewierz, set D) and macrofossil-poor limestones (Żebrownica). The ambocoeliids are also known from presumed autochthonous shell occurrences (typical site), including these transitional to associations with *Spinatrypina* of stratigraphically younger coral buildups (e.g. the *Hexagonaria* Level of Jaźwica, set C; Bilcza, set B). The latter variety is marked by more differentiated brachiopod fauna (schizophoriids, athyrids), small snails, crinoid debris, and ostracods. In the typical locality (see Fig. 31), brachiopods were component of calm-water, muddy *Stachyodes*-biostrome biota, associated with only some euomphalid gastropods and corals. Similar find is known from Zbrza (set A) where the small-sized brachiopod-gastropod fauna co-occurs with single dendroid stromatoporoid coenostea (Kucia 1987).

Desquamatia macroumbonata association of the *Actinostroma* Assemblage.— Typical site: Jaźwica quarry (set H). Full ecologic interpretation of this earliest Frasnian association was given by Racki (1985).

Fitzroyella alata - Parapugnax brecciae association of the Kadzielnia-type Assemblage.— Typical site: Kadzielnia quarry, Kadzielnia Member. This significant bioherm-dwelling fauna was analysed by Biernat (1971) and Racki & Szulczewski (1981); it is the most peculiar innovation within the reef-related Atrypid-Gypidulid Biofacies (Racki *et al.* in press a), widespread in the Frasnian carbonate-complexes. It seems that the mid-slope stromatoporoid-alveolitid-microbial mud mounds from the Gałęzice

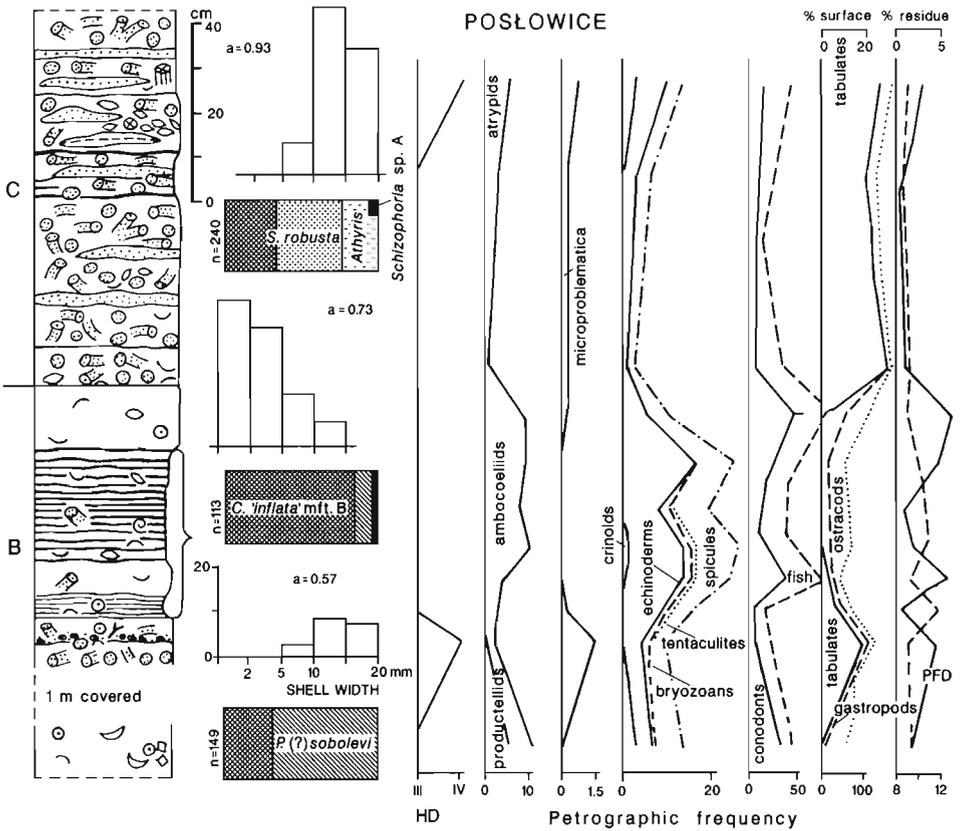


Fig. 28. Lithologic-ecologic succession in the Postowice section (cf. Racki & Racka 1981: Fig. 5; for full sequence see Racki 1993: Fig. 14), with taxonomic composition of brachiopod faunas, size frequency, and articulation index for *Crurispina 'inflata'* (cf. Worsley & Broadhurst 1975: a). Microfacies and residuum shown as in Racki & Baliński (1981): hydrodynamic category (HD); petrographic frequencies in Carozzi's method, petrographic fossil diversity (PFD), and acetic acid resistant residuum content.

Syncline displayed slightly different association than the large buildup from Kielce, especially when regarding atrypids. The difference is well exemplified by similar-age faunas dominated by *Variatrypa* (e.g. Sowie Górki, set G; Jaźwica, set I). However, the samples are too scarce to allow a more conclusive inference. Additionally, the *Variatrypa* monospecific association is sparingly represented already in the Givetian stromatoporoïd biostrome at Łągów.

Coral buildup habitats

A very distinct brachiopod suite is typical of tabulate biostromes. It represents the *Spinatrypina-Thamnopora* Type Assemblage of Boucot

(1975), well known from the Middle Devonian of the Rhenish Slate Mountains (Copper 1966a; Struve 1982), Nevada (Johnson & Flory 1972) and Moravia (Ficner & Havlíček 1978). In the Holy Cross Mountains Devonian, such associations form a transition series from the mid-Givetian 'Amphipora'-dolomites of the Chęciny-Bolechowice area, insufficiently preserved to enable ecologic evaluation, and the coeval Laskowa Góra Beds up to early Frasnian reefs (Racki *et al.* in press a). In contrast, tetracoral buildups only sporadically contain brachiopods, mostly diminutive atrypids.

***Spinatrypina robusta* association** of the *Alveolitella fecunda* Assemblage (Fig. 29).— Type site: Posłowice hill (set C; Fig. 28). This association is markedly limited to the Posłowice-Daleszyce area (Trzemoszna, Marzysz) where it persists from the *Stachyodes*-coral biostromes of the topmost *Stringocephalus* Beds (Posłowice, set A) through the *Alveolitella* Level. Similar tabulate-atrypid faunas appeared in the coeval late Givetian strata of the Wietrznia slope area and Kostomłoty basin (Górno).

Three species invariably play a major role: *S. robusta*, *Crurispina inflata* (morphotype B) and *Athyris* sp. ex. gr. *A. concentrica*. They are distributed very unevenly and clustered ambocoeliids were recovered from the bottom surface of the *Alveolitella*-biostrome set at Posłowice. Rare species comprise schizophoriids, some reticulariids(?) and biplanate strophomenids (Filonowicz 1973).

The brachiopods display fairly large sizes (15–25 mm) and pedunculate to reclining modes of life, except for the free-lying schizophoriids. The index atrypids were presumably fixed to the coral colonies (cf. Copper 1967a; Johnson & Flory 1972) and their mostly flattened-widened shells argue for active laminar currents in the biotope. Delicate athyrid frills served either to stabilize the soft substrate (Wallace 1978) or to facilitate feeding current circulation (Zorn 1976). The ambocoeliids, as well as athyrids, belong to common associates of many Devonian tabulate mounds and biostromes (Bielskaja 1960; Ivanova 1962; Copper 1966a).

***Spinatrypina comitata* association** of the *Hexagonaria-Alveolites* Assemblage.— Typical site: Stokówka hill (set B). The main occurrence is the lumachelle intercalation in the Stokówka section, although elsewhere the atrypids occur frequently in small clumps. Rugose and tabulate corals of the *Hexagonaria* Level are quite different from those of probably coeval association with *S. robusta*.

In the typical section, the atrypids (*S. comitata*, rarer *Desquamatia* sp. A) constitute above 90 per cent of the collection. Minor elements include *D. globosa globosa* (morphotype A), *Tenticospirifer* cf. *utahensis*; at the nearby Zegzelogóra (set B) also sparse ambocoeliids, cyrtospiriferids and reticulariids were gathered.

Most of the species belong to the pedunculate and reclining type, and immature individuals prevail among atrypids. *Tenticospirifer* might represent a micromorphic variety. Furthermore, *D.* sp. A exhibits a tubular type

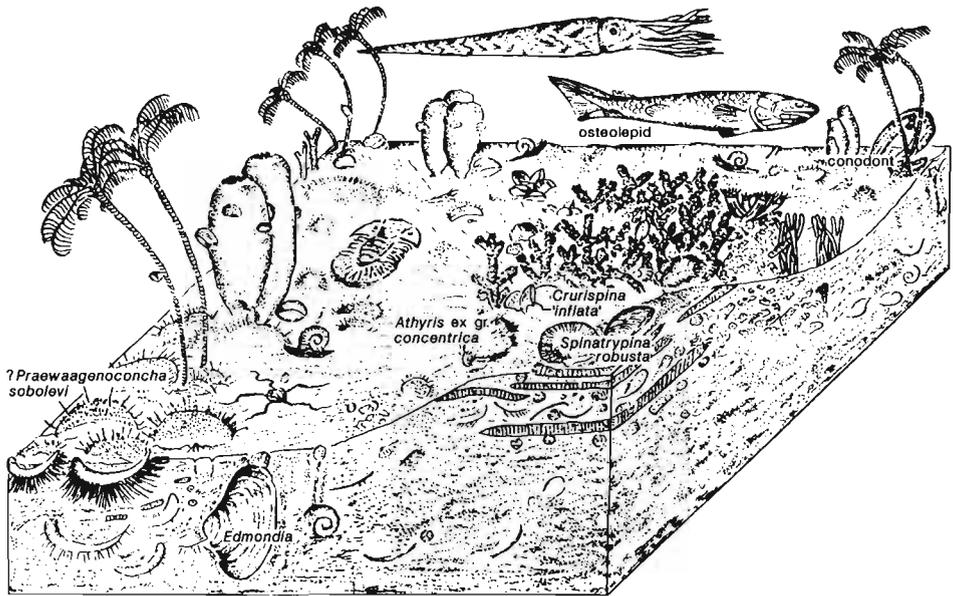


Fig. 29. Idealized biotope reconstruction of the Late Givetian *Praewaagenoconcha(?) sobolevi* and *Spinatrypina robusta* associations of the Echinoderm and *Alveolitella fecunda* Assemblages within the Sitkówka bank complex.

of ribbing homeomorphic (cf. Copper 1967a, 1978) to reef-dwelling genus *Desatrypa*.

The environment of the community under discussion was subject to much stronger hydrodynamic activity and intraformational reworking than in the case of other *Spinatrypina* groupings. A gradation toward the ambocoeliid association (e.g. in *Stachyodes*-*biorudite* at Bilcza) and links to biostrome portions enriched with Tabulata clearly point to such controlling factors. It seems that the brachiopods occupied periodically abraded parts of the biostromal shoal fringing the Chęciny intershoal basin.

***Spinatrypina ex gr. tubaecostata* association** of the *Thamnopora* Assemblage.— Typical site: Sitkówka-Kostrzewa quarry (topmost set C). Small individuals of *Desquamatia*, less than 15 mm long, were identified in several coral-*Stachyodes* biostromal layers of the upper part of the Sitkówka section (see also Sobolev 1911; Filonowicz 1968). More numerous *Spinatrypina* occurs solely in two topmost layers where larger specimens of *Spinatrypina* (up to 18 mm) are associated with *Desquamatia* aff. *macroumbonata*, sporadic cyrtospiriferids and reticulariids. Marly intercalations yield numerous juvenile atrypids (Fig. 14N), ambocoeliids, and the monoplacophoran(?) *Bellerophon*. Siltite matrix of the tabulate coral-bulbous stromatoporoid biostrome contains sponge spicules and echinoderm remains. These characteristics, together with good preservation of the shelly fauna, indicate a quiet, possibly more deeper-water conditions.

Intershoal to open shelf habitats

More or less open marine environments of the evolving Chęciny intershoal area justify the intense brachiopod colonization. Distinguished assemblage groups correspond to the brachiopod niches proposed by Wallace (1978) and McGhee (1981).

Atrypid assemblage group

This suite records a large part of intershoal ecosystems resulting mainly from a wide distribution of expansive and eurytopic species *Desquamatia globosa*.

***Desquamatia globosa* Assemblage.**— Typical site: Góra Zamkowa (set F). Racki & Baliński (1981) described this unit from the type locality of the nominal species, but it is recognized in most outcrops of the Chęciny Beds. Several coquinite intercalations and one 70 cm thick shell bed are exposed in a pit at the middle part of Góra Zamkowa. This micrite bed forms the middle part of a cycle similar to that in the set F, i.e. it was preceded by sorted crinoid grainstones, and followed by fossil-poor wackestones. The main peculiarity of this diminutive *Desquamatia*-dominated assemblage is the participation of *Devonoproductus sericeus* (the pit and southern slope; up to 15 per cent of the fauna) and *Productella* sp. (western quarry).

A close, but more diverse assemblage, including cyrtospiriferids, chonetids, ambocoeliids and coarsely-costate *Spinatrypa*, is established in a co-occurrence with *D. globosa* in the Sosnówka-Zegzelogóra area. There are at least three atrypid-bearing levels, with 1-2 shells per square decimeter, rich in reef-builders in places, and these probably correspond to the low-density atrypid occurrences in the set B of Góra Zamkowa.

The lowest and above 0.5 m thick atrypid bed B-I at Sitkówka-Kostrze-wa is marked by high shell density, up to 5 specimens per square decimeter, and similar associated biota and taphonomic characters as the levels from Chęciny described by Racki & Baliński (1981). The nodular, dark pyrite-rich mudstones and wackestones probably originated in a rather quiet, mud-rich environment.

The monospecific fauna with *D. globosa aequiconvexa* is only known from the bed B-II of Sitkówka, although several other subordinate occurrences are poorly exposed in the higher part of the set B in this profile. The enclosing sediments are similar to those from the main Sitkówka luma-chelle B-I. The low shell convexity and suberect beak suggest adaptations to the life on soft bottoms with still preserved abilities of shell reorientation by the pedicle (see Richardson 1981).

The higher part of the Sitkówka section (set B₂) is marked by *D. globosa sitkowkensis*. The atrypids are quite numerous, up to 2-3 shells per 100 cm², in several platy beds of calcilutites and calcisiltites with many shaly interbeds. The site is characterized by a high frequency of sponge spicules, echinoderm remains and small snails, as well as by the presence a rare

Spinatrypina and smooth spiriferids. *D. g. sitkowskensis* exhibits long frills (Fig. 9F) to compensate for significant (in comparison to *D. g. aequiconvexa*) shell thickness on an unstable sea floor as noted by Ivanova (1962) and Copper (1966a; see also Thayer 1975). The great percent age of disarticulated shells is probably an effect of intense bioturbation. The bedding plane of one such layer bears many shells in reversed positions, showing reoriented shell axes in response to bottom currents occasionally acting on this generally stagnant habitat. The distribution of growth lamellae suggests that the atrypids rapidly slowing down growth of shell after the initial phase of higher rate.

***Iowatrypa timanica* Assemblage.**— Type site: Rzepka hill, eastern quarry. Coquinite partings are scattered throughout several beds, typically 2.5-5 m thick. Embedding the rocks are calcisiltites and calcarenites of subnodular appearance with unnumerous gastropods, crinoid ossicles and tentaculites *Dicricoconus* (Hajłasz 1993). The greatest shell concentration was found in spiculite wackestone impoverished in other skeletal grains.

Representatives of *Iowatrypa* show features of a pedunculate ecologic type, but gerontic globose forms have lived in reclining mode employing the elongated hinge margin, flattened shell and shortened frills for stabilization. Distribution of epizoan microcornids, observed on 15 per cent of the shells (Fig. 11E) chiefly on the dorsal valve, may point to growth in the reversed shell orientation. Sporadic are cases of post-mortem colonization of the hosts on both valves including commissure. The habitat of the assemblage resembles that of stratigraphically older faunas with *Desquamatia*. The flourishing of the atrypid populations within lower-energy environments of the Chęciny area was invariably connected with periods of more intense circulation as indicated by frequencies of tentaculites and conodonts in the same deposits.

Productid assemblage group

These mostly productellid-dominated level-bottom faunas are widespread in the Middle and Late Devonian epeiric seas (Racki *et al.* in press a), but are surprisingly scarcely represented in the region under discussion.

***Praewaagenoconcha(?) sobolevi* association** of the Echinoderm Assemblage (Fig. 29).— Type site: Posłowice hill (set B₁). This characteristic fauna occurs in crinoid-brachiopod bioturbated wackestones. In the upper part of the set there is a gradual transition into impoverished ambocoeliid fauna (Fig. 28) of charophyte meadows (Racki & Racka 1981). The productellids make up to 75 per cent of all brachiopods. They are accompanied by *Crurispina 'inflata'* (morphotype B), abundant remains of echinoderms, sponges, microcornids, gastropods, ostracods, semitextulariid foraminifera, fish, and lingulids.

In coeval strata in Marzysz productellids are found in lighter and more argillaceous deposits that interfinger with tabulate biostromes. Other

brachiopods and macrofaunal remains are rather poor, and only a few costate spiriferids, lingulids, and chonetids(?) have been found.

As known from elsewhere (Grant 1966; Muir-Wood & Copper 1960), juvenile productids fixed themselves by the pedicle or spines to elevated organic objects like crinoids, sponges, or algae. Adult individuals dropped down and lived semi-infaunally with the shell stabilized in the semi-fluid sediment with the aid of a dense brush of spines (Rudwick 1970). Different shell sizes of the productellid populations suggest a soft bottom and stressful conditions in the Marzysz area. Lowly biconvex shells of the associated ambocoeliids may also reflect the restrictive bottom setting.

P.(?) sobolevi fauna is a relict of diverse open shelf biota populating sheltered, muddy biotopes. Apart from dominant sessile faunas comprising different-level filter-feeders ranging from elevated crinoids and sponges through semi-infaunal productelliids, to infaunal lingulids and bivalves, there were numerous vagile animals, alleged vagrant predators and soft-bodied deposit-feeders. It is suggested that the bioturbators facilitated disarticulation of brachiopod shells, especially ambocoeliids. Remarkably, a similar productellid '*P. lachrymosa* Conrad 1842 was linked with ambocoeliids in the diverse open marine *Ambocoelia-Cariniferella* Community, reported from the late Frasnian delta complex of New York by McGhee & Sutton (1981).

***Productella* assemblage.**— This monospecific fauna is limited to poor exposures of the highest Chęciny Beds at the eastern ending of Góra Zamkowa hill, although single productelliids are known from other sites, mainly in the *Desquamatia* assemblages. Taphonomic and lithologic data suggest that this fauna was ecologically close to the *Iowatrypa timanica* Assemblage of similar age. Probably it was confined to the part of the Chęciny basin displaying less stable bottom conditions. The large size of the productelliids characterizes non-reefal biotopes (Brousmiche 1973).

Cyrtospiriferid assemblage group

The spiriferids form two local intershoal assemblages, although they commonly occur as minor elements in many other units (Racki & Baliński 1981). Possibly, in the Frasnian sites at Słopiec and Jaworznia a euryhaline (cf. McGhee 1976) back-reef cyrtospiriferid association could also be distinguished.

***Tenticospirifer lagoviensis* assemblage.**— Typical site: Łagów, *Tenticospirifer* Level. The brachiopods occurs in 1.5-2 m thick complex of incipiently dolomitized wavy-bedded grey calcilutite (Fig. 30). Macrofossils, i.e. snails, crinoid remains, amphiporids, clams, are of patchy distribution.

Such characters of the cyrtospiriferid shell as expanded hinge margin and flat interarea with open delthyrium indicate a complex style of life, maybe with the pedicle acting as a tethering device (Rudwick 1970). The

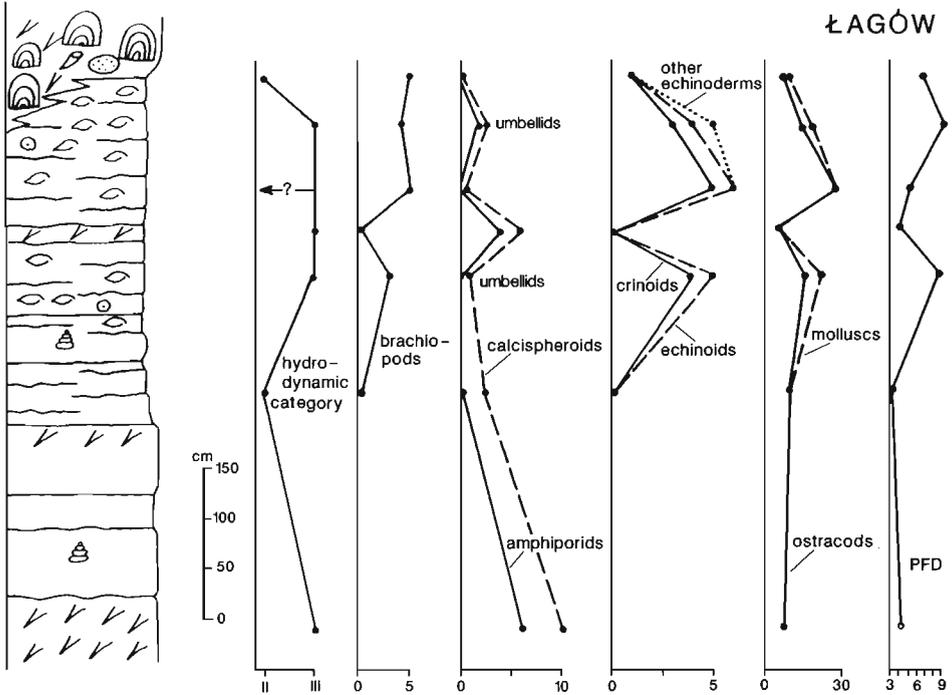


Fig. 30. Lithologic-ecologic succession of the Late Givetian *Tenticospirifer* Limestone Level at Łagów. For explanations see Fig. 28.

tenticuloid shell shape is interpreted by Sorokin (1978: p. 203) as an adaptation to life on more firm substrates.

An intershoal nature of the intermittently agitated muddy biotope is evident owing to many lagoonal exotic biotic elements (amphiporids, calcispheres). This was probably a relatively shallow-water part of the sea directly adjacent to the stromatoporoid-coral mounds. Belskaya (1960) described similar community relations from the Frasnian sea of the Kuznetsk Basin. Rare cyrtospiriferids occur commonly also in the reefal to lagoonal strata of the area (Samsonowicz 1917; Kotański 1959).

Cyrtospirifer assemblage.— This fauna is known solely from the lower Chęciny Beds, especially in the Stokówka section (set C). Similar assemblage, coeval with the Łagów fauna above, might coexist with the stratigraphically slightly older rhynchonellid assemblage in the Jaźwica Member. The low density (ca. 1 shell per square dcm) of mostly disarticulated shells is established in a thin calcisiltite interbed among thicker disphyllid biostromes. Minor cyrtospiriferid occurrences (Stokówka, set E; Góra Zamkowa, set B) are also associated with rugosan intercalations. The bivalves, in particular pterinopectinids, mostly holothurian eleutherozoans, monaxonic demosponges, gastropods, and ostracods constitute the remaining fauna.

The cyrtospiriferid peri-biostromal biotope was probably deeper-water, and stagnant in comparison to that from Łagów, with bottom sediments extensively reworked by bioturbators. This assemblage shows some analogies to the extant brachiopod-bivalve-echinoderm community from the shallow ocean near New Zealand described by Willan (1981).

Other assemblages

Two aggregations with *Crurispina* and *Rhipidiorhynchus* represent peculiar faunas of the Jaźwica Member, chiefly developed in the Bolechowice facies (Racki 1993). Some new data on the well known (Biernat & Szulczewski 1975; Racki 1986a) *Phlogoiderhynchus polonicus* Assemblage are also presented. Remaining Frasnian faunas, such as chonetid-dominated one from the highest Chęciny Beds, await better exposures to be studied.

***Crurispina* 'inflata' association** of the *Crurispina*-microcornid Assemblage.— Type site: Jaźwica quarry (set B; Fig. 31). More than 2 m thick set of platy to subnodular burrowed calcilutites with irregular marly partings contains this characteristic and widespread fauna.

Diminutive sizes and rather strong convexity of the ambocoeliid suggest a dwarf morphotype possibly in a response to sinking at semifluid substrates (cf. Belskaja 1960). The gradual reduction of shell size and specimen frequency toward the top of the Jaźwica Member seems to be an effect of increasing bioturbation and lowering bioclasts content, e.g. crinoid debris. There are factors usually influencing a high juvenile mortality (Richards & Bambach 1975). Shell configurations are suggestive (cf. McGhee 1976) of reversed life position and of a weak pedicle.

The greatest development of the ambocoeliid populations coincides with the first stage of the Late Givetian flooding in the most open marine conditions. Similar monospecific ambocoeliid assemblages flourished in the later Givetian phases too (Racki & Racka 1981) as evidenced particularly by set D at Góra Zamkowa. The unit is an equivalent of the *Ambocoelia* Assemblage of Boucot (1975) common in the deeper open-shelf seas of the North American Givetian and Frasnian (Bray 1971; McGhee 1981) but also e.g. in the Eifel area (Struve 1964; Faber *et al.* 1977).

***Rhipidiorhynchus* assemblage**.— Typical site: Góra Zamkowa, top part of the Jaźwica Member. The coarsely-ribbed, rostrate rhynchonellids show only very localized distribution. In the type locality they occur as scattered clumps in a thin layer of crinoid-gastropod packstone with abundant remains of echinoderms, ostracods, conodonts, and rare brachiopods including varied spiriferids, productellids and pugnacids. There are gradations toward the ambocoeliid and possibly cyrtospiriferid faunas. A suitable, open marine habitat with the sea floor rich in skeletal grains is inferred. Pedunculate to reclining modes of life in intermitently agitated waters are usually assumed for such looking rhynchonellids (McGhee 1976, 1981). The brachiopods played significant role in some Frasnian level-bottom, more nearshore assemblages (Racki *et al.* 1992a) with exam-

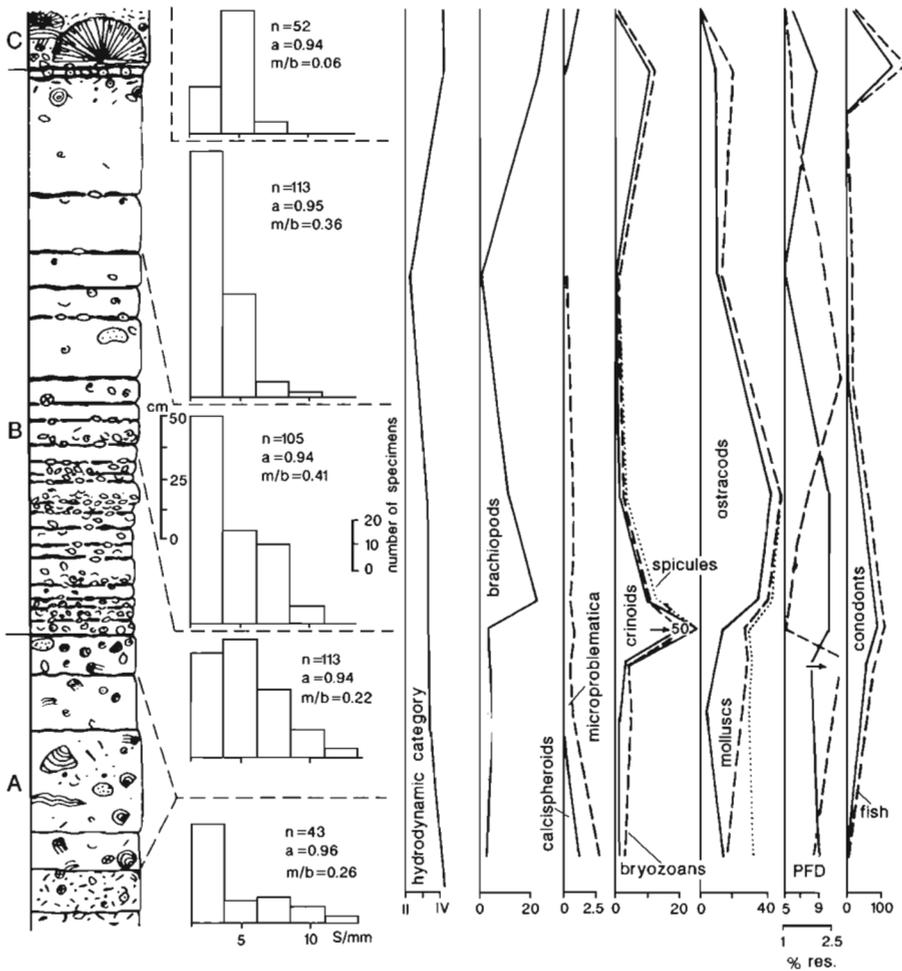


Fig. 31. Lithologic-ecologic succession in the section of the Late Givetian Jazwica Member (Bolechowice facies) at the stratotype (set B); sequence of size distribution for *Crurispina inflata* is shown; m/b – microconchid-gastropod/brachiopod ratio. For other explanations see Fig. 28.

ples from delta-complexes like *Camarotoechia-Cyrtospirifer* community of McGhee (1976).

***Phlogiderhynchus polonicus* Assemblage.**— The new data from the sections of Jazwica-Góra Łgawa, Kowala Quarry and Góra Zamkowa give an insight into the variation within this widely distributed Early-Middle Frasnian assemblage of Racki (1986b). The oldest brachiopod occurrences in the *Phlogiderhynchus* Marly Level point to diversified fauna with many small-sized atrypids, rhynchonellids, athyridids (?*Biernatella*) and spiriferids contrasting with essentially monospecific, stratigraphically younger *P. polonicus* occurrences, with merely single atrypids at Sosnówka and Góra Zamkowa. The fauna is best known from the Jazwica section, where in the

marly nodular and platy micritic beds (see Racki 1993: Fig. 24) at least 15 species occur dominated by *Iowatrypa*-like atrypids. On the other hand, coeval micrite strata of Dębska Wola contain quite different assemblages with *Eleutherokomma*, ?*Biernatella* and small *Hypothyridina* species; the index *P. polonicus* was found at another outcrop (Kawczyn; Kucia 1987). The composition of the earliest Middle Frasnian brachiopod faunas appears rather complex, even on the scale of the Chęciny-Zbrza basin. This diversity has been confirmed for the northern periphery of the Kielce Region, in particular in the rhynchonellid-dominated faunas with *Flabellulirostrum* and pugnacids in the Wietrznia sections (Makowski *in* Racki *et al.* in press a).

Brachiopod faunal dynamics

Assemblage structure *versus* sedimentary regimes

The articulate brachiopods were very successful colonizers in the Devonian carbonate biotopes of the Holy Cross Mountains, with the exception of extremely shallow-water and/or turbulent ones. The most expansive groups are characterized by the presumably most effective spiral lophophores (cf. Fürsich & Hurst 1974).

The changing with time (Fig. 32) 'reefal' associations of varied organic buildups differed significantly from coeval level-bottom assemblages of both lagoonal and open-marine environmental nature. They were more differentiated and contain usually 3 to 6 species, but at least 22 in Kadzielnia-type fauna, with several specialized and in all likelihood endemic species (?8 in Kadzielnia). The ecologic and evolutionary peculiarity of the reef-type biotopes of the Devonian shelves was reported by Torley (1934), McLaren & Norris (1964) and Caldwell (1971), being discussed more broadly by Racki *in* Racki *et al.* (in press a).

Intershoal-dwelling brachiopods formed pioneer assemblages facilitating further settlement by stromatoporoid-coral communities (ecological feedback of Kidwell & Jablonski 1983), even if examples of real ecologic succession are difficult to recognize. Reduced sizes, and short life-spans (4-8 years for ambocoeliids, judging from the number of growth lines) are combined with high initial growth rate (40 to 60 per cent of the mean size by the first year) resulting in probably early sexual maturity, maybe during 1-2 years. These characters, as well as in some cases extensive juvenile mortality, point for r-selection of opportunistic species (Levinton 1970; Goldman & Mitchell 1990). The predominance of small, smooth and thin-shelled species is suggestive (cf. Fürsich & Hurst 1974; Vogel 1980) of life conditions to some extent comparable with deep-water regimes which influence sharp energetic budgets (Alexander 1977; Faber *et al.* 1977), as well as pedunculate habit developed through paedomorphosis (Goldman & Mitchell 1990).

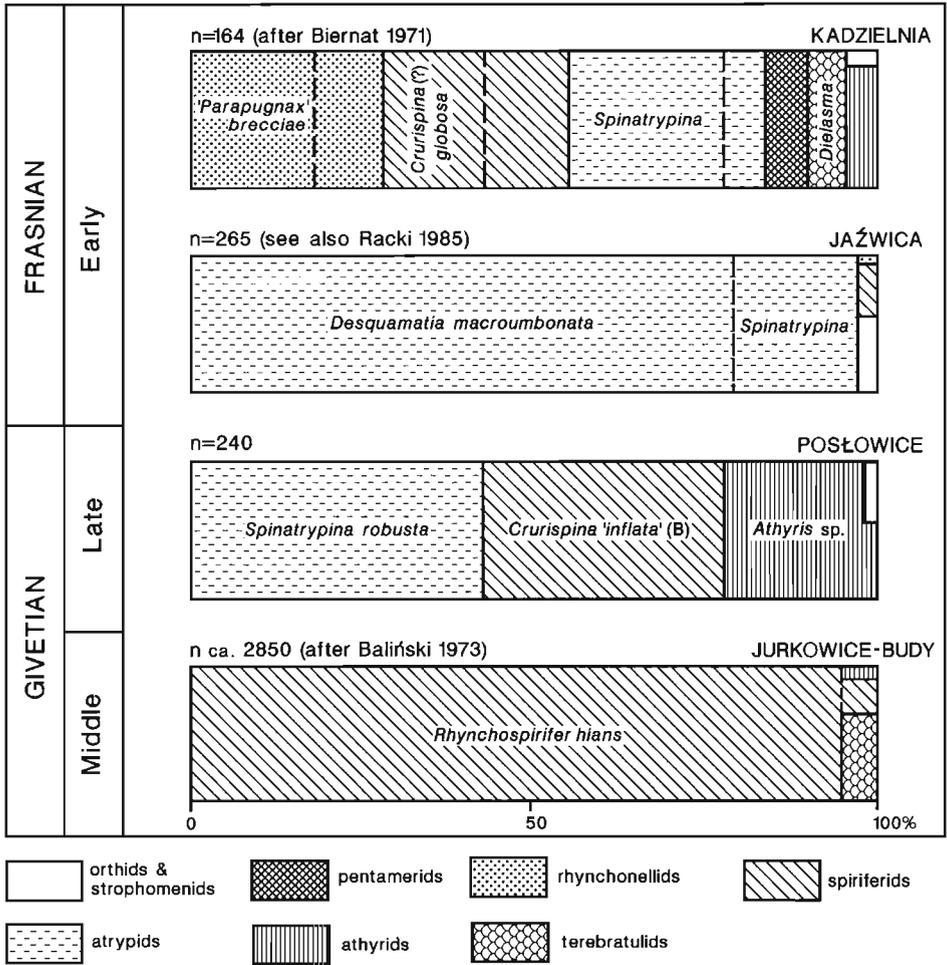


Fig. 32. Taxonomic composition changes of the reef-dwelling associations near the Givetian/Frasnian boundary.

A far simpler ecologic structure is typical for restricted-marine, lagoon-dwelling oligohaline(?) brachiopod assemblages, proper to vast Devonian carbonate platforms (Racki 1986a). In more stable intershoal low-energy habitats (Racki & Baliński 1981) locally fairly complex benthos thrived, as evidenced in particular by *Praewaagenoconcha(?) sobolevi* and *Crurispina 'inflata'* assemblages; the most diversified one (*Rhipidiorhynchus*) comprises at least 8 species. Many features of shell like sculpture with spines and frills, thick valves with complex fabrics, enlarged size up to 3-4 cm, in some cases relatively low initial growth rate and long life span (e.g. in atrypids; cf. Copper 1982), indicate K-selection of some species. External recruitment induced by fluctuating salinity seems to be widespread, especially in assemblages with right-skewed size distributions (Figs 29, 31; but see Cadée 1982 for other explanations).

As claimed by Valentine (1971), a limited taxonomic diversity characterizes biotas developing under rich and/or varying resources. Abundant source of nutrients supported abundant suspension-feeders, with strong epifaunal tiering (cf. Walker 1972), which is evident in brachiopod niches. It seems that the Devonian carbonate biotopes were of high primary production, in vast lagoonal areas resulting in eutrophication (Racki 1986a)

Brachiopod events and biogeography

The general succession of the brachiopod faunas reflects strictly the developmental stages of the Kowala Formation that were controlled by sea-level fluctuations (Racki 1986b, 1993). Instead of biozones (Racki 1988: Fig. 5), the assemblage replacement is here arranged in six brachiopod intervals (B.I. 1-6; Fig. 33), following the concept of 'faunal intervals' of Johnson (1977, 1990; see also stringocephalid levels of Struve 1992).

The two-step intrusion of the brachiopods into the Holy Cross area was preceded by improved conditions of water circulations at the previously hypersaline shelf. In the great colonization events probably joined with the If and Ila Transgressive-Regressive (T-R) Cycles *sensu* Johnson *et al.* (1985), the leading pioneer role played by cosmopolitan giant terebratulids, represented by ecologically exclusive populations (cf. Caldwell 1971) of stringocephalids and rensselandiids. They formed shelly banks in lagoonal and peri-'reefal' environments within the vast Givetian bank of the all southern Poland. The *Rhynchospirifer hians* association, dwelling stromatoporoid shoals, marked the first expansion of the ambocoeliids, while the as oldest *Spinatrypina* was linked with deeper-water, more open-marine thamnoprid thickets.

The next stages of the brachiopod succession were marked by ambocoeliid proliferation in intermittenly agitated, varying in salinity lagoonal biotopes (*Ilmenia(?) elatior* Assemblage), and deep-water, open shelf environments (*Crurispina 'inflata'* fauna). The Late Givetian flooding (IIb) is recorded by the introduction of several immigrants to the part of the Kielce shoal region, mostly from the Kostomłoty-Lysogóry basin domain (atrypids, productellids, chonetids, athyrids) as stated by Racki *et al.* (1985). This pattern contrasts with the more extraregional nature of next immigration waves. There are significant differences in brachiopod faunas between the Połowice and Bolechowice facies within the Jaźwica Member, and the former is marked by multispecific, peculiar assemblage with *Praewaagenoconcha(?) sobolevi*. This differentiation continued next in unlike atrypid faunas related with biostromal fringe and intershoals of the Chęciny and Sitkówka basins, and it is visible even in the joint species in the morphotypes of *C. 'inflata'* and subspecies of *D. globosa*.

Biostromal biotopes, developing as a result of continuous shallowing, supported various brachiopod associations dominated by *Spinatrypina*. This was the beginning of the atrypid thriving, with a locally important

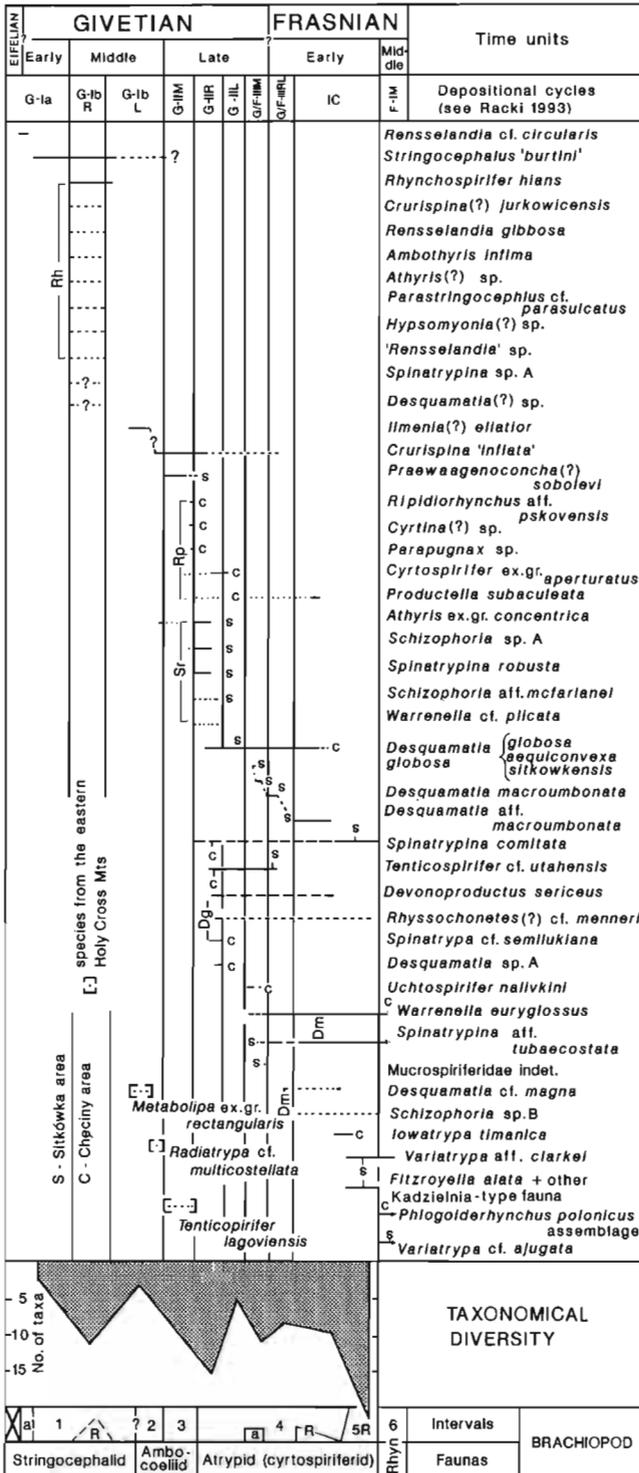


Fig. 33. Stratigraphic distribution, diversity and faunal intervals (see Racki 1988; Fig. 5) of brachiopods in the Givetian to early Frasnian of the southern Holy Cross Mountains. Ecologic groupings: Rh - *Rhynchospirifer hians* (includes also fauna of the Dziewki Limestone), Rp - *Ripidiorhynchus* aff. *pskovensis*, Sr - *Spinatrypina robusta*, Dg - *Desquamatia globosa*, Dm - *Desquamatia macroumbonata*. Interval units signed with 'R' refer to the brachiopod succession in 'reefal' facies, whilst the level '4a' corresponds to *Uchtospirifer nalikini* range.

cyrtospiriferids. The links between different species of tabulates and atrypids are remarkable, and the strict association between *Spinatrypina robusta* and *Alveolitella fecunda* is typical of the northwestern part of the region. The burst of *Desquamatia globosa* in the peri-biostromal and intershoal zones characterizes the Givetian/Frasnian boundary interval (Atrypid-Crinoid Level) being a period of biotic stagnation within the Sitkówka bank complex. The general regressive conditions, interrupted by an epeirogenic event and periodic deepening, stimulated a wide distribution of the atrypid banks incorporated in distinct cyclic environmental changes in the Chęciny area (Racki & Baliński 1981). However, this pattern is difficult to identify in the more stable regimes of the Sitkówka basin. Morphologic conservatism of *D. globosa* from the Chęciny basin contrasts with more progressive changes of the species in the Sitkówka section. This may be a reflexion of reduced sizes of the populations in the geographically semi-restricted Sitkówka basin. Similar development of allopatric populations seems also to characterize other brachiopods from this part of the region like manifested by *Praewaagenoconcha(?) sobolevi*. Finally the reef habitat was reached by descendants of *D. globosa*, such as *D. macroumbonata* (cf. Racki 1985).

Increasing biogeographic differentiation is notable in the course of sedimentary evolution of this carbonate shelf, and a significant separation is visible when the late Givetian and Frasnian faunas of the Holy Cross Mountains and Cracow area (Baliński 1979) are taken into consideration (see also Racki *et al.* in press a). This is even true for the eastern versus western parts of Holy Cross Mountains, especially during the basal transgression of the IIb Cycle. Far more diverse faunas of the Givetian to Frasnian boundary beds occur in the more normal marine regimes of the northern flank of the Kielce platform. They are dominated by atrypids, gypidulids and schizophoriids, and followed by various rhynchonellid assemblages during early Frasnian deepening pulses (Godefroid & Racki 1990; Racki *et al.* in press a). The latter bio-event was expressed also in the more localized southern area, but within less diverse faunas with *Phlogoiderhynchus polonicus*.

The presented developmental pattern seems to be useful for the ecological assesment of brachiopod faunas from the Givetian to Frasnian carbonate complexes elsewhere. In particular, eustatic fluctuations are shown as a primary control on brachiopod distribution, and deepening events were the main disruptive environmental factors in their ecologic evolutionary history (cf. Johnson 1990; McGhee *et al.* 1991).

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Streszczenie

Fauna ramienionogowa z dewońskiej serii stromatoporoidowo- koralowcowej (Formacji z Kowali) południowej części Gór Świętokrzyskich zawiera co najmniej 58 gatunków. Atrypidy i spiriferidy Ambocoeliidae są najbardziej szeroko rozpowszechnione. Słabo zróżnicowane, często jednogatunkowe pionierskie zespoły poziomego dna („level-bottom”) kolonizowały otwartomorskie i śródplyciznowe środowiska późnożyweckiego sitkówczańskiego kompleksu ławicowego („bank complex”) i dymińskiego kompleksu rafowego franu, jak i niektóre lagunowe biotopy stringocefalowej ławicy biostromalnej starszego żywetu. Asocjacje zamieszkujące budowle organiczne były bardziej zróżnicowane i wyspecjalizowane. Dynamika faunistyczne ramienionogów była kontrolowana w pierwszym rzędzie przez cykle eustatyczne i ewolucję środowiskową szelfu węglanowego. Generalnie była to cztero-etapowa sukcesja od fauny stringocefalowej przez ambocelidową, atrypidową i (lub) cyrtospiriferidową po rynchonellidową.

Dwadzieścia dwa gatunki są przedstawione, a z nich *Praewaagenoconcha(?) sobolevi* sp. n. i 2 podgatunki *Desquamatia globosa (aequiconvexa i sitkowkensis)* zaproponowano jako nowe. Nadto, opisano 2 słabo poznane gatunki Güricha (1896), *Tenticospirifer lagoviensis* i *Ilmenia(?) elatior*.